

DEVELOPMENT OF DIONAEA MUSCIPULA

I. FLOWER AND SEED. II. GERMINATION OF SEED AND
DEVELOPMENT OF SEEDLING TO MATURITY

BY
CORNELIA MARSCHALL SMITH

Baltimore, Maryland

1931

Reprinted for private circulation from

THE BOTANICAL GAZETTE, Vol. LXXXVII, No. 4, May 1929; and Vol. XCI, No. 4,

June 1931

PRINTED IN THE U.S.A.

DEVELOPMENT OF DIONAEA MUSCIPULA

I. FLOWER AND SEED. II. GERMINATION OF SEED AND
DEVELOPMENT OF SEEDLING TO MATURITY

A DISSERTATION SUBMITTED TO THE BOARD OF UNIVERSITY STUDIES OF THE JOHNS HOPKINS UNIVERSITY
IN CONFORMITY WITH THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

BY
CORNELIA MARSCHALL SMITH

Baltimore, Maryland

1931



DEVELOPMENT OF DIONAEA MUSCIPULA

I. FLOWER AND SEED¹

CORNELIA MARSCHALL SMITH

(WITH PLATES XX-XXIV AND THREE FIGURES)

Introduction

This paper presents the results of a somewhat detailed study of the flower and seed development of the sole known species of *Dionaea*. A great number of researches have been published dealing with this extremely interesting insectivorous plant, since its original description in a letter of September 23, 1768, to LINNAEUS by JOHN ELLIS (17), but not one of these papers embodies an adequate study of its flower and seed development, and of the germination of the seed.

Dionaea was introduced into Kew Garden by WILLIAM YOUNG (15) in 1768. From that time forward botanists have been interested in the plant, primarily, however, in the movement and digestive powers of the leaf. EDWARDS (15) called attention to the fact that "the small spines, mentioned and figured by ELLIS, are the only irritable points, and that any other part of the leaf may be touched with impunity." CURTIS (9) and CANBY (5) made some of the earliest recorded observations on the insectivorous habits of *Dionaea*, as it grew in its native habitat near Wilmington, North Carolina. Although OUDEMANS (30) examined the leaves histologically, and noted the absence of nyctitropic movements, his report was chiefly concerned with observations on the sensitivity of the leaves.

Between 1874 and 1877 numerous papers on this plant were published. SANDERSON (36) demonstrated the similarity between the contraction of a leaf of *Dionaea* and that of the muscle of an animal in response to electrical stimulation. In 1875, DARWIN (11) not only gave a brief description of the roots and the enlargement of the stem from which the roots spring, and a detailed description of the leaves, but also reported the results of many interesting ex-

¹ Botanical contribution from the Johns Hopkins University, no. 100.

periments which he performed on the latter. Further, he concluded that the closure of the leaf is due to the contraction of a layer of cells on its upper surface. BALFOUR (1) discussed irritability, contraction, secretion, digestion, and absorption in *Dionaea*. He suggested that the spiral thickenings and their elasticity might play an important rôle in the nature and cause of contraction. It was upon the investigations of the anatomy and physiology of the leaf made by KURTZ (26), that MUNK (28) based his work. Although the major portion of the latter's research is concerned with an attempt to explain the action of the leaf from an electrical standpoint, he points out the additional fact that the sensitive hair is divided into two parts, a lever and a base, and that the base alone is capable of receiving stimuli. The results obtained and reported by DARWIN from his experiments on the leaves of *Dionaea* served as an impetus for the anatomical investigations of the vegetative organs of the entire plant by FRAUSTADT (18). Two other papers dealing with the mechanism which produces the movement of the leaves of *Dionaea* were published during this period respectively by DE CANDOLLE (6) and BATALIN (2).

Both GOEBEL (19) and MACFARLANE (27) described and figured the sensitive hairs of *Dionaea*, but the most recent, as well as the most detailed, description of them is that by HABERLANDT (22). Another paper of interest is that of DEAN (12), who, after studying *Dionaea* under native conditions, suggested that it would be more appropriate to call the plant "ant or beetle catcher" than to call it "fly-trap," because of its evident "specialization for the capture of ground insects." That the mechanism which causes the movement of the leaves has proved perplexing, is evidenced by the number of researches that have been and are still being conducted on the subject. The most recent papers offering an explanation of the movement of the leaves have been published by BROWN and SHARP (3), BROWN (4), and GUTTENBERG (21).

Dionaea can be propagated both by seed and by cuttings of the rootstock. HOLM (25) figures and briefly describes the germination of the seed. Although KURTZ states that it had long been a common practice among gardeners to propagate *Dionaea* by means of cuttings made from the inflorescence or flower stalk before the flowers

open, it was not until 1892 that this type of vegetative propagation was described and figured (HARSHBERGER 23, 24).

This brief summary includes the more important papers which have dealt with *Dionaea*. Several others, primarily of taxonomic interest, will be referred to later.

Habitat

Dionaea is a monotypic genus, indigenous, as reported by DARBY (10), CHAPMAN (7), and SMALL (37), to the wet sandy savannahs of eastern North Carolina and eastern South Carolina. The herbaria of the United States National Herbarium, the Missouri Botanical Garden, the New York Botanical Garden, Field Museum of Natural History, the Academy of Natural Sciences of Philadelphia, and the Gray Herbarium include specimens from the following localities in North Carolina: Wilmington, Burgaw, Lake Catherine, Bladen County, Bolton, Scott's Hill, Fayetteville, Dixon, and Hallsboro; and from Georgetown, South Carolina. Professor COKER informs me that he is publishing (8) a map which gives the distribution of *Dionaea*.

The writer visited eastern North and South Carolina the second week in April, 1928, for the purpose of seeing and collecting *Dionaea* in its native habitat. Plants were found growing near Wilmington in an open space in the pines, associated with *Drosera rotundifolia*, *Pinguicula lutea*, *P. elatior*, *Iris verna*, *Sarracenia purpurea*, and *S. flava*. At numerous other habitats from which *Dionaea* had been previously collected by various persons no plants were found, due no doubt to the late spring.

Material and methods

The plants of *Dionaea* used in this study were collected from one of its habitats near Wilmington, North Carolina. The material was shipped in living condition, and then either at once or after being established for some weeks in a greenhouse was fixed in a solution containing 2.5 cc. of glacial acetic acid and 6 cc. of commercial formalin to 95 cc. of 50 per cent alcohol. After dehydration it was imbedded by the usual paraffin method, cut in 5-10 μ serial sections, and stained on the slide. The stain used for the greater part of the work was Haidenhain's iron-haematoxylin. Flemming's triple stain

of safranin, orange G, gentian violet, and the double stain of safranin and light green were sometimes employed, however.

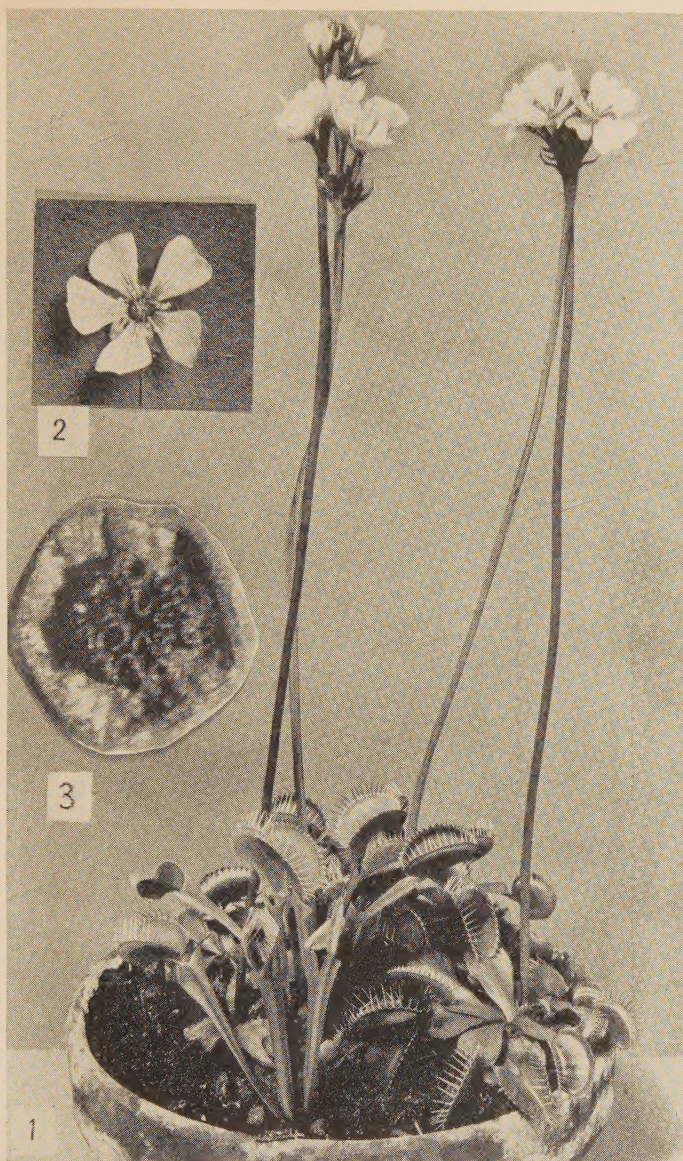
DEVELOPMENT OF INFLORESCENCE

In the early spring, the apex of the sympodial, perennial rhizome of *Dionaea* sends up successive aerial leaves. When from eight to twelve leaves have been developed, a leafless floral axis begins to push out of the terminal bud of the short, horizontal rhizome. Plants collected in North Carolina on April 15, 1927, and examined in Baltimore on April 18 showed scapes 2-3 cm. long. Plants collected April 8, 1928 in the field 2 miles from Wilmington just off the New Bern road possessed floral axes 1-2 cm. in length. When the scape is mature, it may reach 20 cm. or more in height. This axis of the mature flower stalk or scape is about 4 mm. in diameter, and bears a cyme of from two or three up to twelve or fourteen flowers (fig. 1). Not more than four or five flowers of a cyme are open at one time. The flower lasts for about three days.

Each flower has five small green, elliptical, persistent sepals pointed at the apex; five white, cuneate petals notched at the apex; eleven to fifteen stamens (usually fifteen); and a single, compound pistil composed of five carpels (fig. 2). This radially symmetrical, pentacyclic flower develops essentially in the normal manner, the five members of each perianth cycle being synchronous in origin and the different cycles appearing in the usual sequence.

STAMENS AND POLLEN GRAINS

The third and fourth cycles of organs to be differentiated in the flower are composed of stamens. Members of the last formed, epipetalous cycle are often doubled (fig. 6A, B). PAYER (33) was the first to point out that the stamens of *Dionaea* develop in two whorls. He states, however, that the alternipetalous stamens appear interior to and before the epipetalous stamens; and with regard to the number of stamens developed in each whorl he says, "Rarement chacun de ces verticilles n'est composé que de cinq étamines; le plus souvent on en compte plus de cinq, parce que à la place d'une il s'en développe deux." Moreover, in fig. 19, pl. 38, he shows a young flower in which the alternipetalous stamens are doubled, whereas in fig. 20, pl. 38, he shows a slightly older flower in which the epipetalous



FIGS. 1-3.—Fig 1, plants showing different types of leaves, mature scapes, and cymose inflorescence (note wasp captured by leaf of plant on right); reduced one-half; fig. 2, flower with 5 sepals, 5 petals, 14 stamens, and pistil composed of 5 carpels; slightly reduced; fig. 3, receptacle of mature fruit with cup-shaped bolsters of placentar tissue (photographed by A. F. SKUTCH); $\times 15$.

stamens are double. Later, in describing the stamens of *Dionaea*, EICHLER (16) says, "Nach PAYER gehören dieselben 2 ursprünglich 5 zähligen Kreisen an, von denen der alternipetale zuerst entsteht; bei Ueberzahl findet Dédoublement statt, *namentlich im epipetalen Quirl*" (fig. 88 C)." In this figure (p. 224) EICHLER has indicated the "dédoublement" of the epipetalous stamens which he accredits to PAYER. An examination of PAYER's description and figures, however, makes it clear that he believed that either the alternipetalous or the epipetalous stamens could undergo "dédoublement." Although the portion of EICHLER's statement which I have italicized agrees with the facts, it has been wrongly attributed to PAYER. DIELS (13), RENDLE (34), and others cite PAYER for this explanation, which, however, is not found in PAYER but in EICHLER. Further proof of EICHLER's figure may be had by following from their source the course of the vascular bundles of the stamens of young flowers. If this is done, it is found that when the flower has more than ten stamens, one or more of the five vascular strands which supply the five epipetalous stamens are divided, and that two epipetalous stamens have developed in place of one where the strand is divided. Fig. 6A shows a cross-section of the receptacle of a young flower containing fourteen stamens, in which five vascular strands respectively of the outer alternipetalous and of the inner epipetalous stamens are visible. Fig. 6B shows a similar section of the same flower 60 μ nearer the apex, in which four of the five vascular strands of the epipetalous stamens are divided. If, on the other hand, the flower develops but ten stamens, the five outer alternipetalous stamens alternate with the five inner epipetalous stamens, as is shown in fig. 5C. Although most of the taxonomists report ten to twenty stamens for *Dionaea*, none of the flowers which I have as yet examined possessed more than fifteen. I have been unable, therefore, to determine what the arrangement of the stamens would be in a flower developing more than fifteen stamens.

Each stamen originates as a protuberance involving dermatogen and periblem. As the protuberance grows it pushes upward, and gradually broadens above the slender base (figs. 5, 7, 9). The upper enlarged end is the anther, in which four microsporangia develop; the slender base becomes the filament.

¹ Italics mine.

The microsporangia develop in the usual manner. A cross-section of a young anther shows usually a single primary archesporial cell in each of the four corners immediately beneath the epidermis. In the upper right corner of fig. 8 are shown two primary archesporial cells, a relatively rare case. A longitudinal section shows that, in reality, each cell seen in transverse section is one of a row of from five to seven cells extending the full length of the anther. Each cell of this row divides into an outer parietal and an inner sporogenous cell. By radial and periclinal divisions, the primary parietal cells then give rise to from three to five concentric layers of wall cells (fig. 10).

Subsequent differentiation among the wall cells results in the formation of the tapetum, the "middle layers," the endothecium, and the epidermis. In following the further history of each layer, changes are seen to occur first in the innermost layer of wall cells, the tapetum. Its cells enlarge, become granular, and often binucleate (figs. 16, 21). In enlarging, the tapetal cells encroach upon the "middle layer," crush, and finally absorb the one or two rows of cells of which the middle layer is composed (figs. 21, 23). Next the cells of the endothecium begin to increase in size. A transverse section of a microsporangium (fig. 23) made at this stage shows the cells of the endothecium to be approximately as large as those of the epidermis, and the tapetum greatly reduced as it is being gradually absorbed in the maturing of the spores. Finally the tapetum completely disappears, the walls of the endothecium become prominently thickened in bands, and the cells of the epidermis disintegrate (fig. 25). This same figure shows the weak place in the sporangium wall, where the slit, by means of which the pollen grains may escape, is to be formed.

By successive divisions of the primary sporogenous cells forty-eight to sixty microspore mother cells are formed. These mother cells have increased, by the time of synizesis, from a diameter of $15-17\ \mu$ to one of $25-30\ \mu$. Concurrently the diameters of their nuclei enlarge from a diameter of 10 or $11\ \mu$ to one of 15 or $17\ \mu$. The nucleoli do not change in size, remaining about $4\ \mu$ in cross-section. Due to the fact that the nucleus of the spore mother cell increases in size as the cell matures in preparation for meiosis, however, the

nucleolus is proportionately larger in the early stages. In a single microsporangium all nuclear changes occur almost simultaneously (fig. 16), but the four sporangia of the same stamen do not always show the same stage of development.

The nuclear phenomena which occur in the spore mother cells preparatory to and during the formation of tetrads may be described as follows. Small chromatin granules or prochromosomes, similar to those described by ROSENBERG (35) in *Drosera* and by OVERTON (31) in *Thalictrum*, *Calycanthus*, and *Richardia*, are visible in the resting nucleus. They are arranged in pairs of units lying side by side on the linin threads, and are distributed about the periphery of the nucleus, close to the nuclear wall (fig. 11). As the nucleus enters the prophase (fig. 12), the chromatin threads become more distinct and then pass into the synizesis contraction (fig. 13). The paired chromatin threads become massed together at one side of the nuclear cavity in synapsis. Usually the nucleolus lies adjacent to but distinct from the chromatin mass. In some cases, however, it is surrounded by filaments of chromatin.

When the threads of the synaptic knot loosen up, the loops of the spireme formed appear to be double, with paired chromatin granules scattered along them (fig. 14). The spireme then segments into fifteen pairs of bivalent chromosomes, which are found scattered throughout the nucleus (fig. 15). Some parts of the chromosomes stain more deeply than other parts, as is shown in fig. 15. As a consequence of gradual shortening and thickening, the chromosomes acquire a compact form and draw closer together (fig. 17). The nuclear membrane is visible about the chromosomes in diakinesis. Fig. 16 shows a longitudinal section of a microsporangium in which the cells are rounded up and more or less separated from one another (segments of the original walls being still visible between some of the cells), and in which the nuclei of all the microsporocytes are in diakinesis.

The microsporocytes of a sporangium adjacent to the one shown in fig. 16 have advanced a stage further; the spindle is formed for the first meiotic division. Fig. 18 shows the V-shaped chromosome tetrads as they appear in metaphase with the spindle fibers attached. The double character of the chromosomes, as they move apart in the anaphase, becomes clearly discernible (fig. 19). Four nuclei, each

having fifteen haploid chromosomes, result from the second division, which occurs immediately after the first (fig. 20).

Walls appear between the four nuclei (fig. 21), thus cutting out the four microspores of a tetrad. As the microspores mature each develops an outer spore coat, the exine, containing six to eight germ pores, and an inner spore coat, the intine (fig. 23). The exine is composed of an outer layer, made up of slender prismatic elements standing perpendicular to the surface, interspersed among which are longer, pointed prisms or spines; and of an inner layer of apparently homogeneous structure (fig. 26). The two layers when fully developed are of about equal thickness (each $2.5\ \mu$). Because of the prominence of these two layers of the exine in the mature spore, they were at first mistaken for the exine and intine respectively, but on closer examination it was seen that they together make up the exine, and that the intine is a separate, much more delicate coat adjacent to and completely surrounding the protoplast. The intine is very plastic; it becomes more easily distinguishable when it grows out through the germ pores of the exine to form the pollen tube (figs. 25, 26).

In fig. 23 each microspore or very young male gametophyte of the tetrad is shown with its two spore coats incasing a resting nucleus surrounded by vacuolated cytoplasm. This nucleus divides into the generative nucleus and tube nucleus (fig. 25). This is the usual condition of the microspores when shed. In some instances the generative nucleus has already divided, however, forming the two male nuclei. Fig. 26 shows a section through a tetrad of germinating pollen grains as found on the stigma. In each grain the pollen tube protrudes from a germ pore; in two of the pollen tubes a tube nucleus is visible; the male nuclei have not as yet passed into the pollen tube. In the interior of the style can also be seen portions of pollen tubes, identified by their tubular structure and by their reaction to stain. The cell contents of the latter could not clearly be distinguished.

CARPEL AND SEED

The last cycle of members to be formed in the flower is one of five carpels, which, like the stamens, originate as outgrowth from the perilem involving also the dermatogen. The prominence which

gives rise to the carpels is at first convex, then flat (fig. 5), and later concave (fig. 7). The concave structure is divided into five carpels, each of which in turn is differentiated into an upper and a lower region. As the upper portions elongate they curve inward, come into contact with each other, and later coalesce to form a column, known as the style, containing a central styler canal (figs. 9, 27, 32). The end of the style is divided into numerous projections or papillae, composed of cells with large nuclei and dense cytoplasm which later serve as receptive structures for pollen.

In the young flower the papillae curve inward, forming a small knoblike structure, the stigma (fig. 52*A*). When the style has reached a length of about 2.5 mm., these papillose bifurcations of the stigma straighten up, bend outward, and expose the receptive tissue. Any pollen which at this time comes in contact with the stigma may germinate. Fig. 52*B* shows a pollen tetrad on the stigma. Later the papillae of the stigma shrivel and coil outward. They are found in this condition surmounting the dried-up style of the mature fruit.

The wall of the ovary is formed by the coalescing of the lower portions of the five carpels. The term "Parakarpe Gynäceen" has been applied by GOEBEL (20) to the ovary of *Dionaea*, because its carpels are joined by their margins only. As it grows, the cavity in which the anatropous ovules are to develop gradually enlarges (figs. 9, 32, 52*A*). From the floor of the cavity of the very young ovary, numerous erect hypodermal protuberances appear in serial succession, from the inside outward, around the growing point of the flower, as illustrated and described by GOEBEL (20) and as shown in fig. 9. Each protuberance becomes differentiated into a basal stalklike structure, the funiculus, and terminal region, the nucellus or ovule. When the protrusion is about five cells across in transverse section and twenty-five in longitudinal section, the nucellar end becomes slightly curved; and, concurrently the first integument is initiated about its base (fig. 27). External to the first integument a second forms, while the nucellus curves progressively downward beside the funiculus. A longitudinal section of an ovule made at a slightly later stage (figs. 32, 33) shows the ring of tissue of the first integument surrounding all except the apex of the nucellus; and the

second integument, part of which is formed from the funiculus, encircling the first for about two-thirds of its length. The integuments continue to elongate and soon overtop the nucellus, the first integument drawing successively closer together over the nucellus, leaving only a narrow passage way, the micropyle.

Each integument is composed of two or three layers of cells. The layers of the inner integument, except where they overtop the nucellus, consist of thin-walled parenchyma cells which remain unspecialized. In the chalazal end of the ovule, however, some of the thin-walled cells have become disorganized and replaced by air spaces (fig. 63). On the other hand, those cells which overtop the nucellus finally become heavily lignified and form an inner seed cover or lid (figs. 70, 71), which is pushed off in the course of the germination of the seed. This structure resembles that which NETOLITSKY (29) has described in *Drosera rotundifolia*.

Only the outermost layer of cells of the outer integument shows any specialization, the inner layers, with the exception of a group of thickened cells investing the vascular strand, remaining unmodified and difficult to distinguish from the cells of the inner integument. The former develops into an outer protective layer, made up of closely packed, radially arranged, heavy-walled, columnar cells (fig. 63). This might be called the palisade layer, because its cells resemble in form the palisade cells of a leaf; or the cells of which it is composed could be called Malphigian cells, except that the "luminous line" usually present in the latter is wanting in the seed of *Dionaea*. The external walls of the cells become progressively and evenly thickened, whereas the radial walls first become thickened in strips (fig. 63) and later in coalesced bands (fig. 71).

If the mature fruit is examined, it is seen to contain numerous seeds grouped on a basal placenta. EDWARDS (15) describes the seeds and their insertion as follows: "Seeds black, shining, obovate, very acute at the lower end, half buried in the cavities of the honey-combed receptacle." DRUDE (14) says in regard to them: "Samen zahlreich auf der gewölbten Blütenachse central eingefügt." The writer's observations confirm these descriptions, except she finds that the lower end of each seed, even when mature, is only slightly imbedded in a cup-shaped bolster of receptacular tissue. The exact

shape and arrangement of these collars of receptacular tissue are shown in the photograph of a mature floral receptacle (fig. 3). In a longitudinal section of a much younger ovary (fig. 52A) this tissue is seen projecting up about the micropylar end of each ovule.

The single bundle or vascular strand of each ovule develops in the funiculus, which, as has been stated, becomes fused with a part of the outer integument. The strand extends to the chalazal region of the ovule; it shows no tendency to turn or twist in its course. In the young ovule the first vascular tissue to be developed consists of narrow, elongated, densely protoplasmic cells, the procambium (fig. 33). It is from these cells that the xylem, consisting of long, slender, spirally thickened cells, and the phloem parenchyma of the mature strand develop. This mature strand, which is surrounded by a group of thickened cells of the outer integument, measures about $55\ \mu$ in transverse section.

The nucellar tissue within the integuments shows some interesting differentiations. The epidermal cells, except those immediately above the sporogenous cells, form a layer of radially placed, closely packed, thin-walled cells which enlarge immensely and in so doing become more and more conspicuous (figs. 33, 46, 58). They increase from 7.5 to $62.5\ \mu$ in anticlinal length from the time that the spore mother cell is formed (fig. 33) to the time of fertilization (fig. 58). These radially elongated cells completely surround a central strand, four to five cells wide, which extends from the prothallial cells to the vascular strand and is composed of longitudinally elongated cells (figs. 46, 58). Since the latter lie in direct contact with the vascular strand, at the chalazal end of the ovule, it seems reasonable to assume that the prothallial cells receive their nourishment through them.

This enlargement of the nucellar cells resembles that described in *Drosera rotundifolia* by Miss PACE (32), who states further that these cells, together with the air spaces developed in the chalazal region of the ovule, greatly reduce the specific gravity of the seed. The latter statement is hardly true with respect to the enlarged nucellar cells of *Dionaea*, because of the fate of the cells and of the spaces occupied by them. As the embryo develops in *Dionaea* the endosperm encroaches upon the nucellar tissue (fig. 58), disintegrat-

ing and absorbing both the central strand of elongated cells and the encircling radially-attenuated cells (fig. 63). Finally, in the mature seed the cellular endosperm completely fills the space occupied by the nucellus, and also the space occupied by the thin-walled cells of the integuments (fig. 71). As a result the specific gravity of the seed does not decrease but is actually increased.

Since the latest stage of seed development of *Drosera* figured by Miss PACE shows fertilization, it seems reasonable to suppose that she did not follow out the subsequent development of the endosperm and the fate of the nucellar tissue; hence her conclusion that the enlargement of the nucellar cells reduces the specific gravity of the seed is not valid. Further, an examination of a series of slides of *Drosera rotundifolia* made by C. A. PETERS at Ann Arbor, Michigan, and now in the collection of slides of the Johns Hopkins University, shows that the endosperm develops at the expense of the nucellar tissue very much as it does in *Dionaea*.

The single archesporial cell of the megasporangium is set off immediately beneath the epidermis of the nucellus, about the same time that the first integument appears. This cell is easily recognized by its large size and dense protoplasm, as well as by its apical position in the nucellus (fig. 28). It is about $17\ \mu$ in transverse section, and contains a nucleus which has a diameter of $10\ \mu$. By mitotic division (fig. 29) it gives rise to the primary sporogenous cell and primary parietal cell (figs. 30, 31). The latter is concerned with the production of a small portion of the megasporangium wall, but not in the formation of distinct layers of wall cells as is true of the parietal cells of the microsporangium.

The first division of the primary parietal cell is by a radial wall, which is easily discerned when it is perpendicular to the plane of the section (figs. 34, 35). Although it is impossible to follow the subsequent divisions of the individual parietal cells, as they are no longer distinguishable from the adjoining nucellar cells, it is evident that by periclinal divisions two or at most three layers of cells are formed above the sporogenous cells (figs. 44, 48). These layers are at once infringed upon and absorbed by the developing megaspore (figs. 46, 51).

The primary sporogenous cell usually develops directly into a

single megaspore mother cell (figs. 33, 34); rarely there are two (fig. 35). Since no further development of the two mother cells was observed in the several hundred sections studied, it is hardly probable that these ever progress far enough to develop two embryo sacs or embryos in an ovule. The single mother cell, on the other hand, increases in size and passes through nuclear changes similar to those described in the microspore mother cells. Paired prochromosomes, of approximately the same number as the definitive chromosomes, are visible in the resting nucleus. In the late prophase the chromatin threads become more distinct and then pass into the synaptic contraction. Fig. 36 shows the loosening up of the spireme and the paired chromatin centers about which the chromosomes develop. The spireme is then segmented into fifteen pairs of bivalent chromosomes, each of which becomes more distinct as diakinesis approaches (fig. 37). The formation of the spindle and further nuclear phenomena in the division of the megaspore mother cell were not observed. In fig. 47, however, it is evident that the reduced number of chromosomes is present at the second division of the functional megaspore; in other words, there are fifteen haploid chromosomes.

The mother cell divides to form two (fig. 38), then by a second division of one of the daughter cells it forms three (fig. 39); or in other cases both daughter cells divide and four potential megaspores are formed (figs. 41, 42). These four spores are usually arranged in an axial row. That the two daughter cells do not necessarily divide simultaneously to form the tetrad of megaspores is shown by figs. 39 and 40. Three of the four potential megaspores degenerate, leaving but one functional. Usually in *Dionaëa*, as in other angiosperms, the non-functional cells of the micropylar end of the ovule disappear (figs. 44, 48, 49). Fig. 43 shows a single active megaspore with the degenerating cells in the chalazal end of the ovule, an uncommon occurrence. The last vestige of the degenerating megaspores disappears before the eight-nucleate embryo sac is completely organized.

EMBRYO SAC, ENDOSPERM, AND EMBRYO

The embryo sac is initiated with the division of the functional megaspore, after which the daughter nuclei move apart, one going to each end of the embryo sac. The cytoplasm between the nuclei

becomes more and more vacuolated (figs. 44, 45). Subsequent divisions take place rapidly and simultaneously. Fig. 48 shows the four nuclei and fig. 50 the eight nuclei resulting respectively from the second and third divisions; and fig. 49 shows that the third division occurs at the same time in all four of the nuclei resulting from the second one.

One of the four nuclei at each end of the embryo sac, the polar nucleus, migrates toward the center. The three nuclei remaining at the micropylar end form the egg apparatus; the three nuclei remaining in the chalazal end form the antipodal cells (fig. 51). The egg apparatus is quite normal, consisting of two synergids and an egg. Each of the former has a notch, is capped by a filiform apparatus, and contains one or more vacuoles in its lower end (fig. 51). The egg cell has a larger nucleus than the synergids, and usually lies nearer the center of the embryo sac, below the synergids. The two polar nuclei, which come to rest in the middle of the sac just below the egg, are of about the same size, each containing a large nucleolus. The two nuclei may lie side by side at the same level, or one may be nearer the egg and the other nearer the antipodals. They are always surrounded by a mass of cytoplasm, some strands of which extend upward to connect with the layers of cytoplasm that surround the lower end of the egg, while other strands reach to the notches in the synergids. The antipodal cells which are located in the chalazal end of the sac never become conspicuous; they often disappear shortly after they are formed.

Actual fusion of the egg and sperm cells was not observed, although hundreds of sections, made at about the time of fertilization, were examined. Fig. 51 shows the polar nuclei in contact with each other, and fig. 53 shows the polar nuclei in the process of fusion, thus forming the primary endosperm nucleus. In some cases the polar nuclei fuse before, and in other instances after fertilization. Fig. 54 shows the primary endosperm nucleus with its characteristically large nucleolus. The mean diameters of the primary endosperm nucleus and nucleolus are 18 and 8 μ respectively, ascertained by averaging twenty measurements. Referring again to fig. 54, the fertilized egg can be seen below the synergids, the contents of which are entirely obscured by a darkly staining substance, that was probably

introduced with the entrance of the pollen tube. That the synergids do not disappear immediately after fertilization is evidenced by the fact that remains of them and their degenerating nuclei are visible after several divisions of the fertilized egg (figs. 59, 61).

The primary endosperm nucleus divides before the fertilized egg, and its subsequent divisions occur more rapidly than those of the egg. The nuclei resulting from the first and second divisions of the endosperm nucleus are shown in figs. 55 and 57; they are elongated and each contains two or more nucleoli. The egg has not yet divided. The early mitoses occur simultaneously in all nuclei (fig. 56). Later, however, when the endosperm has become multinucleate, the nuclei in one region show a different stage of development from those in other regions of the endosperm (fig. 63).

With the multiplication of the nuclei in the endosperm, the cytoplasm surrounding the former becomes more and more vacuolated; and, as a result of the union of numerous small vacuoles, a single sap-filled central vacuole develops. With this increasing vacuolation the nuclei are caused to assume a peripheral position, a group of them becoming arranged in a funnel-shaped mass near the chalazal end of the embryo sac. From fig. 58 it will be seen that, although the fertilized egg has not divided nor have the synergids completely disintegrated, the endosperm has progressed to the condition just described, the lower funnel-shaped portion of it having already begun its inroads upon the surrounding nucellar tissue. As growth continues this lower end of the endosperm, which acts somewhat as a haustorium, progressively encroaches upon and absorbs the nucellar cells, until it finally comes in direct contact with the vascular strand at the chalaza. A median longitudinal section through the ovule (fig. 63) shows a relatively thin layer of cytoplasm, with free nuclei surrounding a central vacuole and extending from the embryo to the vascular strand. A mass of cytoplasm and nuclei are to be seen in contact with this strand. A surface view of the endosperm, made at the same stage (fig. 64), shows the nuclei about equally spaced in a uniformly distributed layer of cytoplasm.

When free nuclear division has ceased in the endosperm, walls are formed between the nuclei, as a result of which an outer layer of cells is developed about the central cavity (fig. 69). With the

initiation of wall formation, each nucleus of the hundred or more then present becomes surrounded by a somewhat denser mass of cytoplasm, strands of which extend to the encircling cytoplasm of the adjacent nuclei (figs. 65, 66). Each of the connecting strands becomes less dense and more curved as it passes outward from the mid-line between adjoining nuclei. STRASBURGER (38) has described and figured, in *Agrimonia eupatoria*, *Reseda odorata*, and certain other plants, a condition similar to this. The distribution of the cytoplasm about the nuclei at this stage makes it possible to predict that the cell walls will appear in a plane equidistant between neighboring nuclei and at right angles to the connecting strands. The next stage observed is shown in fig. 67. The fibrillae, which had their origin in the connecting strands of cytoplasm, show the equatorial thickenings which later split to form two parallel cell plates (fig. 68). A thin continuous cell wall is soon formed between the two cell plates and the fibrillae begin to disorganize. The cells thus formed now divide and gradually replace the central cavity (fig. 69). Finally the entire embryo sac, except the part occupied by the embryo, is filled with the cellular endosperm (figs. 70, 71).

In contrast to the free nuclear division of the primary endosperm nucleus, the first division of the nucleus of the fertilized egg is accompanied by the formation of a cell wall. This first division is transverse to the long axis of the embryo sac, moreover, and results in the formation of the suspensor and embryo (fig. 59). Of the two the suspensor cell is situated nearer the micropyle, is larger, and tapers toward the micropyle, while the embryo proper is hemispherical. Furthermore, the first division of the suspensor cell usually precedes that of the egg (fig. 60).

The first and second divisions of the embryo are longitudinal and transverse respectively. Fig. 61 shows the four cells resulting from these divisions. The cytoplasm of the cells of the embryo is much denser than that of the suspensor cells. The cells of the embryo continue to multiply, and soon an outer layer of cells, the dermatogen, is cut off by periclinal walls (fig. 70). In the meantime the suspensor cells have divided and formed a cylindrical structure composed of six to eight cells (fig. 70), the ultimate fate of which was not determined. The embryo in the mature seed consists solely of two small

cotyledons and a short radicle (fig. 71). The structure of the embryo becomes further differentiated in the process of germination. It will be more fully described in a second paper, on *Dionaea muscipula*, dealing specifically with the germination of the seed and seedling. The bearing of the facts here recorded on the relationships of *Dionaea* will also be deferred to the second paper for discussion.

Summary

1. The terminal bud of the short perennial rhizome of *Dionaea* forms a scape which bears a cymose inflorescence of from two to fourteen actinomorphic, pentacyclic flowers.

2. The arrangement of the vascular bundles of the stamens in the receptacle of young flowers is considered as further proof of PAYER'S statement that the stamens develop respectively in alternipetalous and epipetalous whorls. Moreover, when more than ten stamens (five in each cycle) develop, the vascular bundle of one or more of the five epipetalous stamens is divided and supplies the additional stamen or stamens. This is not in accord with the view held by PAYER that "dédoublement" may occur in either whorl.

3. The four microsporangia of each stamen develop in the usual manner.

4. In the early prophase of the microsporocytes, of which forty-eight to sixty develop in each sporangium, prochromosomes are discernible.

5. Each of the four nuclei resulting from the second meiotic division of the microsporocyte has fifteen haploid chromosomes.

6. The mature pollen grains hang together in tetrads and each contains six to eight large germinating pores.

7. The "paracarpous" ovary of *Dionaea*, which is composed of five carpels, develops numerous anatropous ovules on a basal placenta, with the tip of each slightly imbedded in a cup-shaped bolster of placental or receptacular tissue.

8. The outermost layer of cells of the second integument forms an outer seed coat of closely packed, radially elongated, heavy-walled, columnar cells; while those cells of the inner integument which overtop the nucellus form a lid or cover which is pushed off when the seed germinates.

9. The single vascular strand which extends to the chalazal end of each ovule shows no tendency to turn or twist in its course.

10. The outer layer of nucellar cells, except where it overtops the prothallial cells, increases enormously in radial dimension, surrounding a central strand of longitudinally elongated cells.

11. By division of the single hypodermal archesporial cell, two or at most three layers of parietal cells are formed above the embryo sac.

12. Rarely more than a single megaspore mother cell is developed; the mother cell divides to form two, then four potential megaspores; the divisions of the daughter cells do not necessarily occur simultaneously.

13. Usually, as in other angiosperms, the three micropylar potential megaspores degenerate and the chalazal one functions. In one instance the three basal spores degenerated and the micropylar one functioned.

14. The embryo sac resulting from three successive divisions of the functional megaspore contains, when ready for fertilization, the usual egg apparatus, polar nuclei, and antipodals.

15. The primary endosperm nucleus usually completes several mitoses before the fertilized egg divides to form the embryo and suspensor.

16. As the endosperm increases it progressively encroaches upon the surrounding nucellar tissue, and by the time that free nuclear division has ceased in the former all nucellar tissue has disappeared.

17. The mature seed contains a small basal embryo, consisting of two cotyledons and a short radicle surrounded by the cellular endosperm.

This study was undertaken at the suggestion of Professor DUNCAN S. JOHNSON, whose generous interest and invaluable direction have been indispensable to its prosecution. My indebtedness to him I cannot too gratefully acknowledge

JOHNS HOPKINS UNIVERSITY
BALTIMORE, MD.

[Accepted for publication July 17, 1929]

LITERATURE CITED

1. BALFOUR, A. G., Account of some experiments on *Dionaea muscipula*. Trans. Bot. Soc. Edinburgh 2:334-369. 1876.
2. BATALIN, A., Mechanik der Bewegungen der insektenfressenden Pflanzen. Flora 60 (neue Reihe 35):54-73; 105-111; 129-154. 1877.
3. BROWN, WM. H., and SHARP, L. W., The closing response in *Dionaea*. BOT. GAZ. 49:290-302. 1910.
4. BROWN, WM. H., The mechanism of movement and the duration of the effect of stimulation in the leaves of *Dionaea*. Amer. Jour. Bot. 3:68-90. 1916.
5. CANBY, W. M., Notes on *Dionaea muscipula*. Gardener's Monthly, ed. by THOS. MEEHAN 1:229-232. Philadelphia. 1868.
6. DE CANDOLLE, C., Sur la structure et les mouvements des feuilles du *Dionaea muscipula*. Arch. Sci. Phys. Nat. 55:400-431. 1876.
7. CHAPMAN, A. W., Flora of the southern United States. 2d. ed. New York. 1887 (p. 37).
8. COKER, W. C., The distribution of *Dionaea muscipula*. Jour. Elisha Mitchell Sci. Soc. 43:221. 1928.
9. CURTIS, W., Enumeration of plants growing around Wilmington, N.C. Boston Jour. Nat. Hist. I. 2:123-125. 1835.
10. DARBY, JOHN, Botany of the southern States. New York. 1855 (p. 236).
11. DARWIN, CHARLES, Insectivorous plants. London. 1875 (pp. 286-320).
12. DEAN, B., *Dionaea*: its life habits under native conditions. New York Acad. Sci. 12:9-17. 1892.
13. DIELS, L., Droseraceae. ENGLER, A., Das Pflanzenreich IV. 112:1-136. 1906.
14. DRUDE, O., Droseraceae. ENGLER and PRANTL, Die natürlichen Pflanzenfamilien III. 2:261-276. 1894.
15. EDWARDS, S., Curtis Bot. Mag. 20:785. 1804.
16. EICHLER, A. W., Blüthendiagramme. Leipzig. 1878 (pp. 224-225).
17. ELLIS, J., Nova Acta Regiae Societatis Scientiarum Upsaliensis 1:98-101. 1773.
18. FRAUSTADT, A., Anatomie der vegetativen Organe von *Dionaea muscipula* Ellis. Cohn Beiträge zur Biologie der Pflanzen 2:27-64. 1877.
19. GOEBEL, K., Pflanzenbiologische Schilderungen. Marburg. 1893 (pp. 57-72).
20. ———, Organographie der Pflanzen. Jena. 1898-1901 (pp. 741-742).
21. VON GUTTENBERG, HERMANN, Die Bewegungsmechanik des Laubblattes von *Dionaea muscipula* Ell. Flora (Neue Folge) 18-19:165-183. 1925.
22. HABERLANDT, G., Sinnesorgane im Pflanzenreich. Leipzig. 1901 (pp. 108-117).
23. HARSHBERGER, J. W., An abnormal development of the inflorescence of *Dionaea*. Bot. Lab. Univ. Penna. 1:45-49. 1892.

24. ———, An unusual method of vegetative reproduction in *Dionaea muscipula*. BOT. GAZ. 44:282-283. 1907.
25. HOLM, THEO., Contributions to the knowledge of the germination of some North American plants. Mem. Torr. Bot. Club 2:57-108. 1891.
26. KURTZ, F., Zur Anatomie des Blattes der *Dionaea muscipula*. Archiv. Anat., Physiol. Wiss. Med. Reichert Du Bois-Reymond. 1876 (pp. 1-29).
27. MACFARLANE, J. M., Contributions to the history of *Dionaea muscipula*. Bot. Lab. Univ. Penna. 1:7-44. 1892.
28. MUNK, H., Die elektrischen und Bewegungs-Erscheinungen am Blatte der *Dionaea muscipula*. Archiv. Anat., Physiol. Wiss. Med. Reichert Du Bois-Reymond. 1876 (pp. 30-122; 167-203).
29. NETOLITZKY, FRITZ, Anatomie der Angiospermen-Samen. LINSBAUER, K., Handbuch der Pflanzenanatomie 10:146-149. 1926.
30. OUDEMANS, C. A. J. A., Over de Prikkelbaarheid der Bladen von *Dionaea muscipula*. Verslagen en Medeldeel. K. Akad. Wetensch. 9:320-436. 1859.
31. OVERTON, J. B., On the organization of the nuclei in the pollen mother-cells of certain plants, with especial reference to the permanence of the chromosomes. Ann. Botany 23:19-61. 1909.
32. PACE, LULA, *Parnassia* and some allied genera. BOT. GAZ. 54:306-329. 1912.
33. PAYER, J. B., Traité d'organogénie comparée de la fleur. Paris. 1857 (pp. 180-188, atlas pl. 38).
34. RENDLE, A. B., The classification of flowering plants. Cambridge Univ. Press. 1925 (pp. 193-199).
35. ROSENBERG, O., Cytologische und morphologische Studien an *Drosera longifolia* × *rotundifolia*. Kungl. Svenska Vetenskapsakademiens Handlingar 43:4-64. 1908.
36. SANDERSON, B., Nature 10:105-107; 127-128. 1874.
37. SMALL, J. K., Flora of the southeastern United States. New York. 1903 (pp. 492-493).
38. STRASBURGER, E., Zellbildung und Zelltheilung. 3d ed. Jena. 1880.

EXPLANATION OF PLATES XX-XXIV

All figures were drawn with the aid of the camera lucida, except figs. 1-3.

FIG. 4.—Transverse section of very young inflorescence; sepals differentiated in all flowers, petals in lowest flower on left only; ×38.

FIG. 5.—Longitudinal section of young flower, showing protuberances giving rise to stamens and carpels; ×38.

FIG. 6.—*A*, transverse section of receptacle of young flower containing 14 stamens, showing the 5 vascular strands respectively of outer alternipetalous and inner epipetalous stamens; *B*, similar section of same flower 60 μ nearer apex, in which 4 of the 5 vascular strands of epipetalous stamens are divided; *C*, similar section of flower developing only 10 stamens, 5 outer alternipetalous

alternating with the 5 inner epipetalous (*s*, sepal; *p*, petal; *a*, alternipetalous; *e*, epipetalous); all $\times 18$.

FIG. 7.—Longitudinal section of flower of about same age as those shown in preceding figure; stamens clavate, carpels concave; $\times 38$.

FIG. 8.—Transverse section of young anther, showing 2 primary archesporial cells in left corner, primary archesporial cell in mitosis in right corner, and primary parietal and sporogenous cells in each of lower corners; $\times 172$.

FIG. 9.—Longitudinal section of flower with stamens in spore mother cell stage and ovules appearing in base of ovary; $\times 38$.

FIG. 10.—Transverse section of single anther; microspore mother cells surrounded by 3 or 4 concentric layers of wall cells; $\times 172$.

FIG. 11.—Single microspore mother cell in early prophase, showing paired prochromosomes and nucleolus; $\times 925$.

FIG. 12.—Nucleus in late prophase; $\times 925$.

FIG. 13.—Nucleus in synapsis; $\times 925$.

FIG. 14.—Nucleus with uniformly distributed, distinctly double spireme; $\times 925$.

FIG. 15.—Spireme segmented; 7 pairs of chromosomes shown; $\times 925$.

FIG. 16.—Longitudinal section of microsporangium, showing binucleate, granular tapetal cells and rounded-off microsporocytes in diakinesis; $\times 172$.

FIG. 17.—Nucleus of microsporocyte, showing chromosomes in diakinesis; $\times 925$.

FIG. 18.—Chromosomes in late metaphase of meiosis number one; $\times 925$.

FIG. 19.—Polar view of anaphase of first meiosis; double nature of chromosomes clearly visible; $\times 925$.

FIG. 20.—Four nuclei, each with 15 haploid chromosomes, resulting from second meiotic mitosis; $\times 925$.

FIG. 21.—Transverse section of microsporangium, showing epidermis, endothecium, "middle layers," and tapetum consecutively surrounding tetrads of pollen grains; $\times 172$.

FIG. 22.—Transverse section of anther, showing relative position of 4 microsporangia; $\times 18$.

FIG. 23.—Detail of single microsporangium: epidermis, endothecium, disintegrating tapetum, and tetrads of pollen grains with germinating pores, nucleus, and vacuolated cytoplasm distinguishable; $\times 172$.

FIG. 24.—Transverse section of almost mature anther, showing position of the 4 microsporangia, and partition wall between adjacent sporangia; $\times 18$.

FIG. 25.—Detail of single microsporangium, showing weak spot where split will occur, endothecium with its thickened fibers, and mature pollen grains; $\times 172$.

FIG. 26.—Tetrad of germinating pollen grains; $\times 715$.

FIG. 27.—Median longitudinal section of young pistil; ovules on basal placenta, surrounding growing point of flower; $\times 38$.

FIG. 28.—Single hypodermal archesporial cell of megasporangium; $\times 715$.

FIG. 29.—Archesporial cell in mitosis; $\times 715$.

FIG. 30.—Primary parietal and sporogenous cells; $\times 715$.

FIG. 31.—Similar section but of somewhat differently shaped cells; $\times 715$.

FIG. 32.—Longitudinal but not quite median section of slightly older pistil; $\times 38$.

FIG. 33.—Detail of single ovule, showing procambium, outer and inner integuments, and megaspore mother cell; $\times 172$.

FIG. 34.—Megaspore mother cell in early prophase, with two parietal cells immediately above; $\times 715$.

FIG. 35.—Similar section, showing two megaspore mother cells; $\times 715$.

FIG. 36.—Nucleus of megaspore mother cell, just previous to segmentation of spireme; $\times 925$.

FIG. 37.—Chromosomes in diakinesis, 15 pairs visible; $\times 925$.

FIG. 38.—Two megaspores resulting from first division of mother cell; $\times 715$.

FIG. 39.—Similar stage; nucleus of one cell in mitosis; $\times 715$.

FIG. 40.—Similar stage; nucleus of each cell in different stage of mitosis; $\times 715$.

FIG. 41.—Similar stage; nucleus of each cell in same stage of mitosis; $\times 715$.

FIG. 42.—Similar stage; 4 nuclei in early prophase; no walls formed between grand-daughter nuclei; $\times 715$.

FIG. 43.—Functional megaspore in micropylar end of ovule; 3 degenerating megaspores in chalazal end (only 2 shown in this figure, third in next section); $\times 715$.

FIG. 44.—Longitudinal section of 2-nucleate embryo sac; nuclei migrated to each end; cytoplasm containing numerous vacuoles; $\times 715$.

FIG. 45.—Slightly older embryo sac; nuclei in diakinesis; one large vacuole in center; $\times 715$.

FIG. 46.—Longitudinal section of ovule containing 4-nucleate embryo sac; inner integument overtops nucellus, leaving only narrow passage way (micropyle); outer layer of nucellar cells begun to elongate radially about central core of longitudinally attenuated cells; $\times 172$.

FIG. 47.—Detail of single nucleus, showing 15 haploid chromosomes; $\times 925$.

FIG. 48.—Slightly different stage but similar section of 4-nucleate embryo sac; non-functional megaspores in micropylar end of sac; $\times 715$.

FIG. 49.—Similar section, showing 4 nuclei in mitosis; disintegrating megaspores in micropylar end; $\times 715$.

FIG. 50.—Eight-nucleate embryo sac; $\times 715$.

FIG. 51.—Mature embryo sac containing synergids, egg, polar nuclei, and antipodals; $\times 715$.

FIG. 52.—A, longitudinal, median section of pistil (just previous to fertilization), showing incurved papillae of stigma, styler canal, and ovules with tips

slightly imbedded in cup-shaped bolsters of placental tissue; *B*, similar section of stigma with two tetrads of pollen grains attached and germinating; $\times 18$.

FIG. 53.—Longitudinal section of embryo sac, showing fertilized egg, and two polar nuclei in process of fusion; $\times 715$.

FIG. 54.—Slightly older embryo sac, showing fertilized egg, synergids containing dark-staining substance, and primary endosperm nucleus; $\times 715$.

FIG. 55.—Fertilized egg and 2 nuclei resulting from first division of primary endosperm nucleus; $\times 715$.

FIG. 56.—Endosperm nuclei in telophase of second mitosis; $\times 715$.

FIG. 57.—Fertilized egg showing 3 of the 4 nuclei resulting from second division of endosperm nucleus; $\times 715$.

FIG. 58.—Longitudinal section of entire ovule, showing radially elongated nucellar cells surrounding central strand of longitudinally attenuated cells, fertilized egg, synergids, and endosperm which is making inroads upon nucellar tissue; $\times 172$.

FIG. 59.—Longitudinal section, showing suspensor cell and hemispherical embryo; $\times 715$.

FIG. 60.—Similar section, mitosis occurring in suspensor cell; $\times 715$.

FIG. 61.—Four-celled embryo; $\times 715$.

FIG. 62.—Somewhat older embryo; dermatogen in process of differentiation; $\times 715$.

FIG. 63.—Longitudinal section of entire ovule, showing 16-celled embryo, outer seed coat with thickened walls, air spaces, and multinucleate endosperm; $\times 172$.

FIG. 64.—Surface section of endosperm shown in preceding figure; nuclei in mitosis surrounded by evenly distributed cytoplasm; $\times 715$.

FIG. 65.—Each nucleus surrounded by denser mass of cytoplasm, strands of which extend to each of neighboring nuclei; $\times 715$.

FIG. 66.—Slightly advanced condition, showing fibrillae between nuclei; $\times 715$.

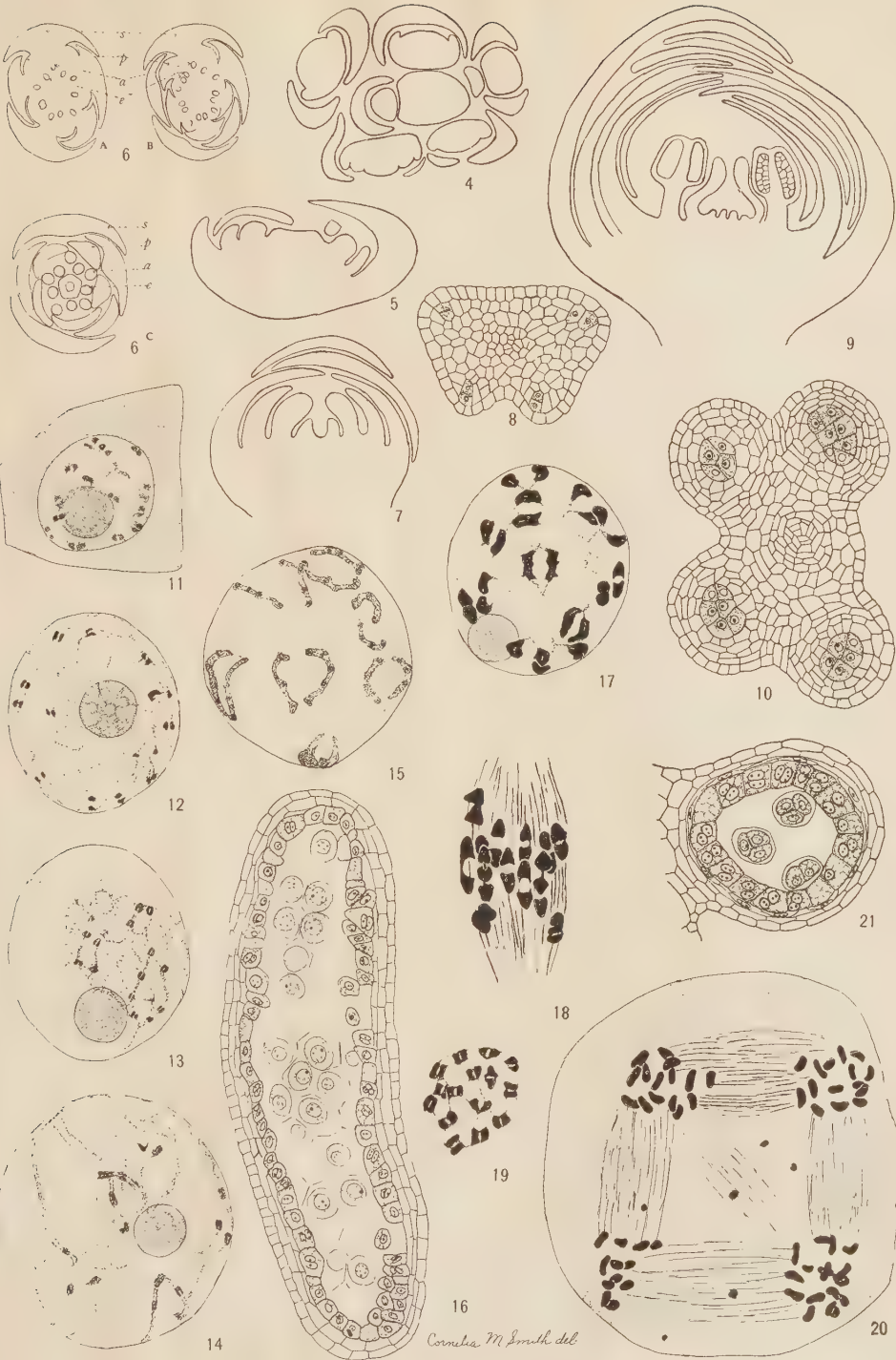
FIG. 67.—Equatorial thickenings on fibrillae; $\times 715$.

FIG. 68.—Parallel cell plates formed by splitting of equatorial thickenings; $\times 715$.

FIG. 69.—Longitudinal section of embryo and endosperm consisting of layer of cells surrounding central sap-filled cavity; $\times 172$.

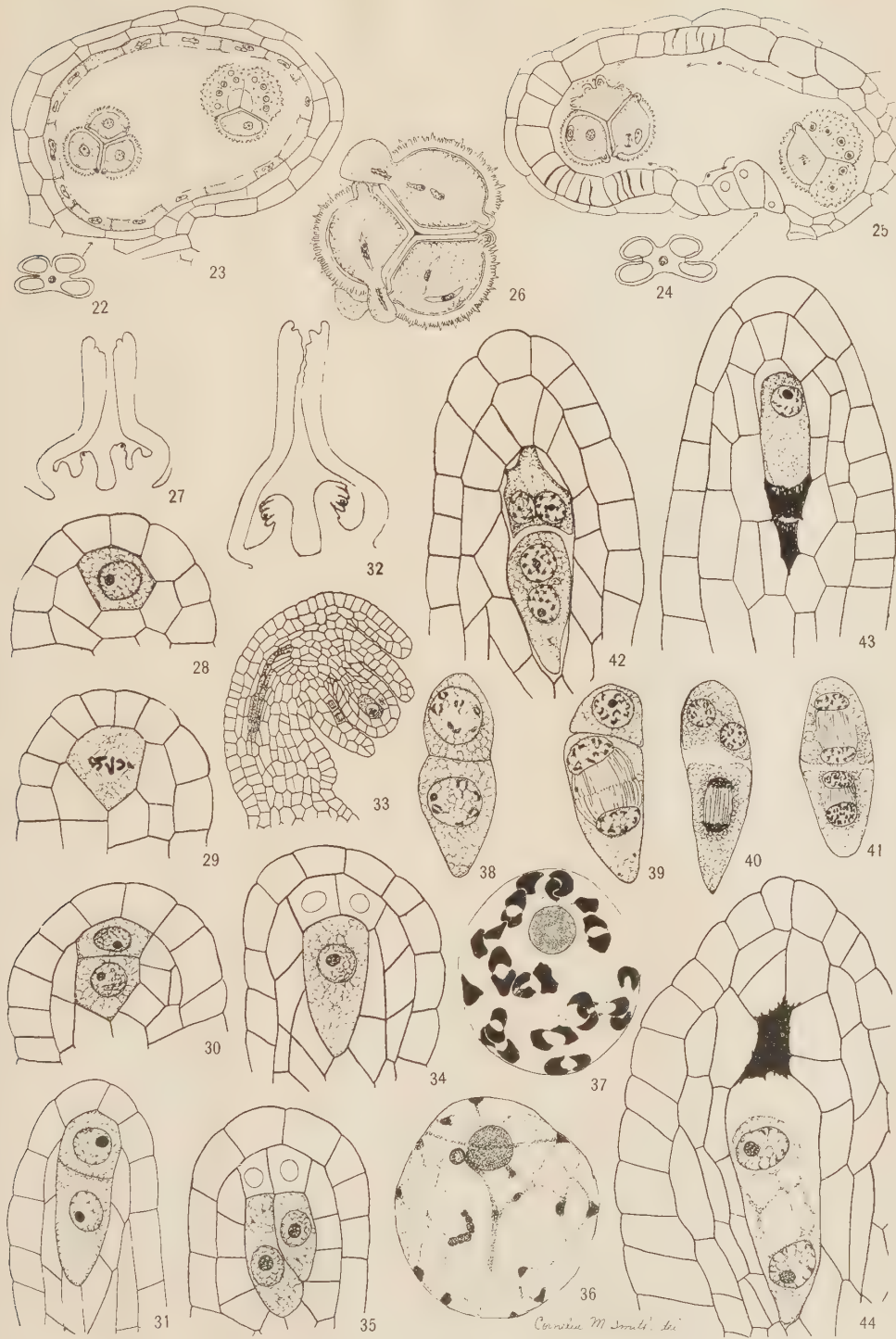
FIG. 70.—Similar section of somewhat later stage, showing seed lid formed by tip of inner integument, and cellular endosperm which completely fills central cavity and surrounds embryo; $\times 172$.

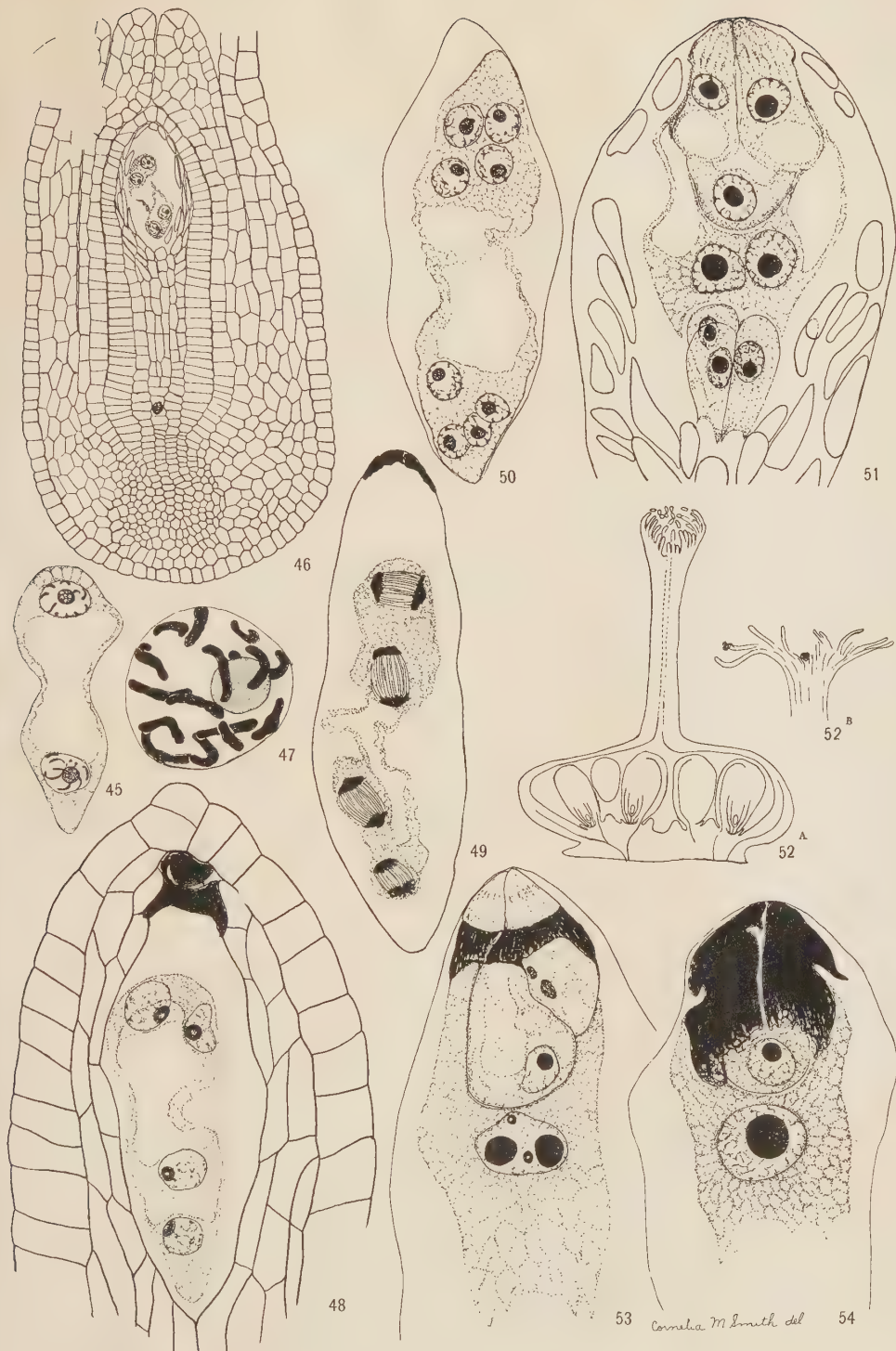
FIG. 71.—Similar section of mature seed, showing embryo consisting of 2 small cotyledons and short radicle surrounded by single layer of cellular endosperm which fills remainder of seed; and thickened bands of cells of outer integument which have coalesced, forming black, shiny seed coat; $\times 73$.



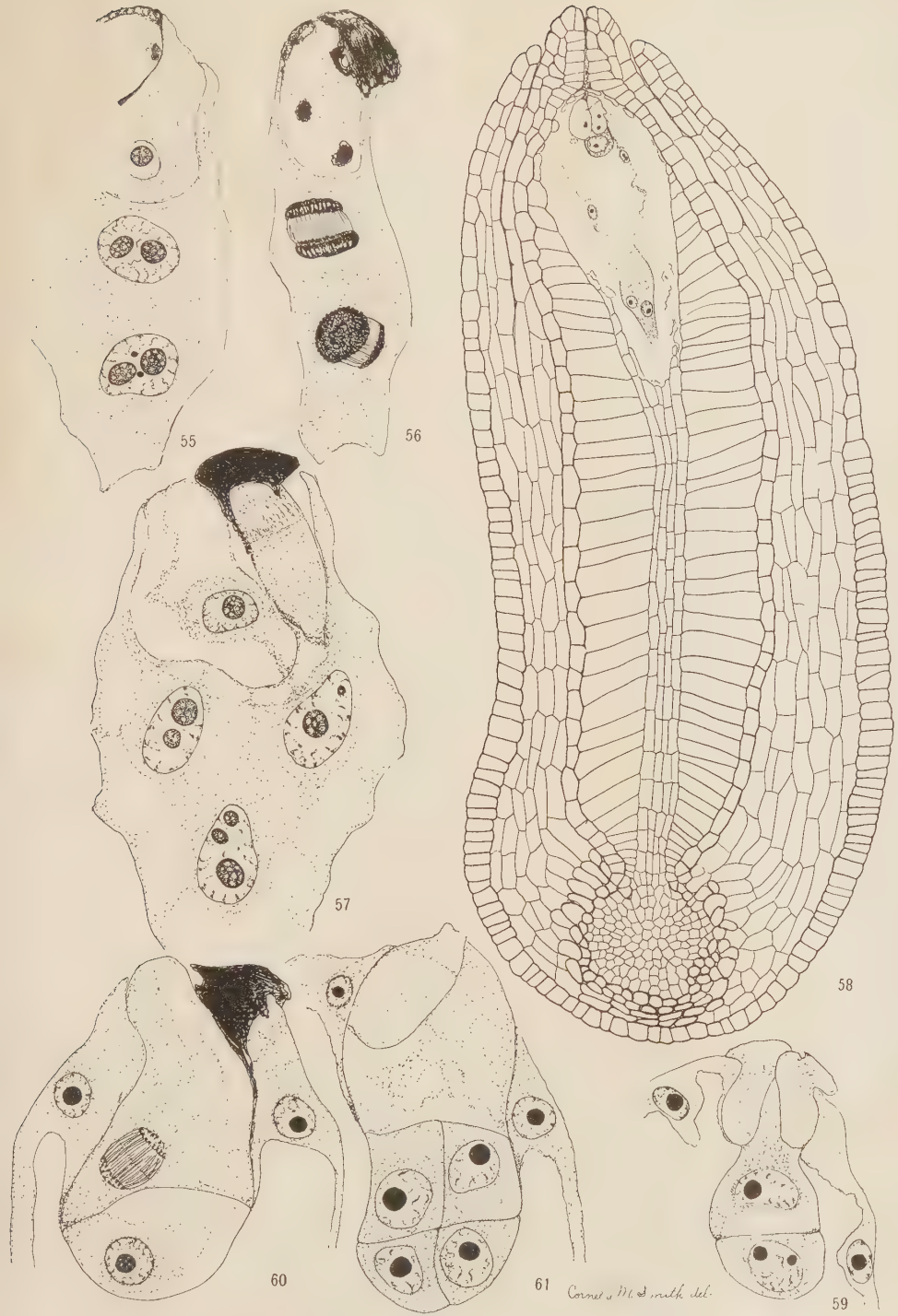
Cornelia M. Smith del.



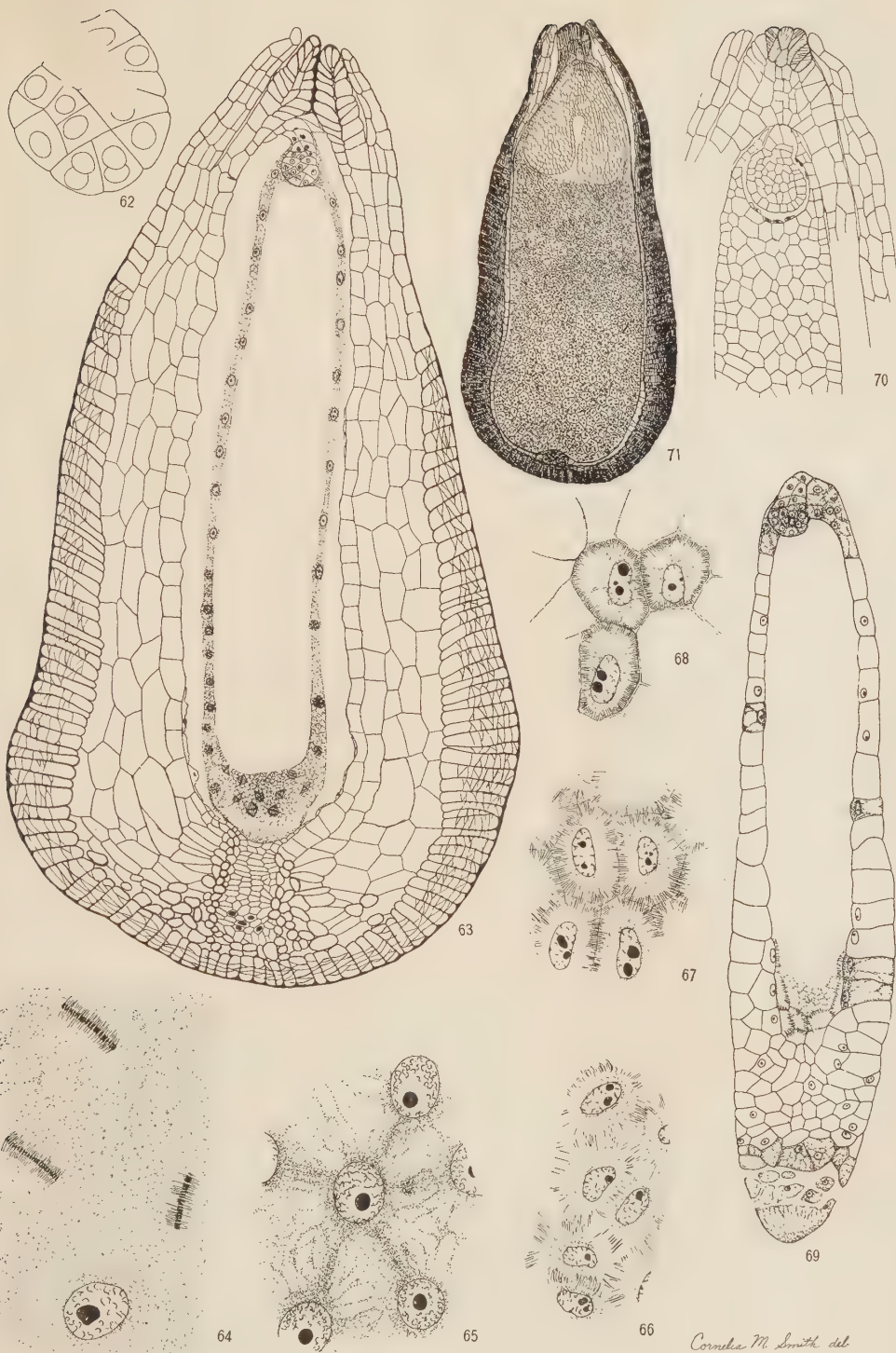




Cornelia M. Smith del



SMITH on DIONAEA



SMITH on DIONAEA

Coriela M. Smith del

DEVELOPMENT OF DIONAEA MUSCIPULA

II. GERMINATION OF SEED AND DEVELOPMENT OF SEEDLING TO MATURITY¹

CORNELIA MARSHALL SMITH

(WITH THIRTY-SIX FIGURES)

Preparation of soil

The seeds of *Dionaea* are difficult to germinate. Of the various conditions under which the writer attempted to grow them, the following proved to be the most successful. The bottom of a porous clay flower pot, 5 inches in height and 6 inches in diameter, was covered with pieces of broken pottery, on top of which was placed a layer of sand and then a mixture, 2 inches in depth, of sand and humus collected from a bog where *Drosera* and *Sarracenia* grew. The seeds were scattered over the surface of the soil, which was sprinkled with water in order to bury them slightly. The flower pot was covered with a plate of glass, taken into a greenhouse, and placed in a concrete tank containing just enough running water to keep the soil within continuously moist. The temperature of the greenhouse was maintained at 25°–35° C. Under these conditions some of the seeds germinated in 10 days, some in 2 weeks, others not until the lapse of 3 weeks, and a number of them had not germinated when the experiment ended.

Mature seed

A longitudinal section of a mature latent seed (fig. 7) shows the broad face of one of the cotyledons, the stem growing point, and the hypocotyl of the embryo. The embryo is surrounded at its micropylar end by a single-layered cellular structure, which fits over it like a cap and extends to the copious endosperm. These structures are invested by a thin inner and a rather thick, black, outer seed coat.

In the writer's previous paper (25), in which the origin and development of the endosperm were traced, it was shown that the endosperm contains a bountiful supply of starch. According to later

¹ Botanical contribution from The Johns Hopkins University, no. 110.



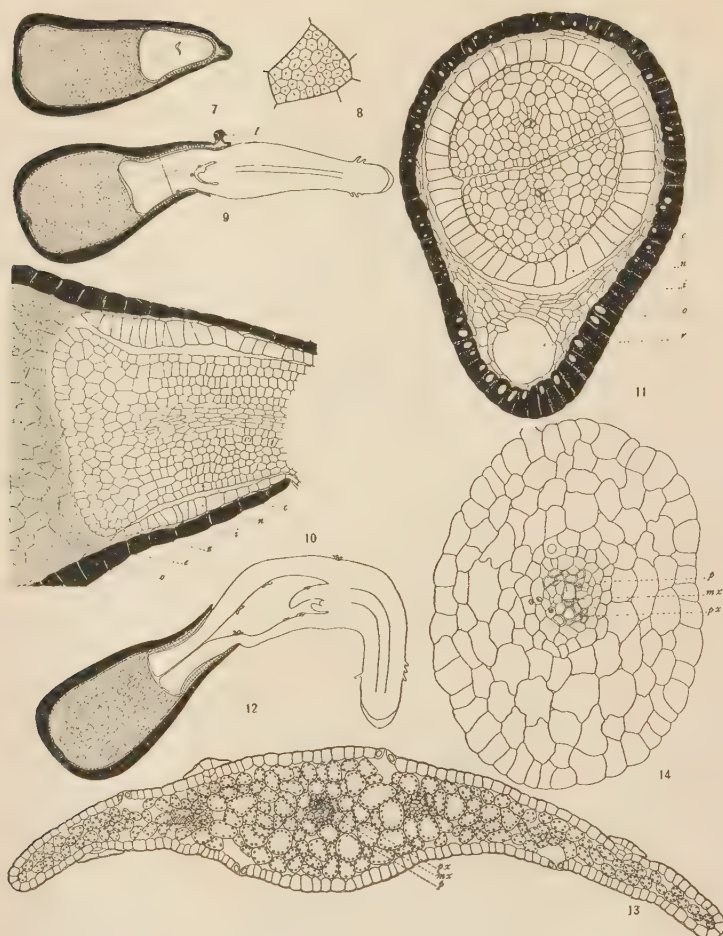
FIGS. 1-6.—*Dionaea muscipula*: stages of development in germination; $\times 10$

study, the starch grains are usually pentagonal or hexagonal in cross-section (fig. 8), and vary from 5 to 7 μ in diameter. The persistent nucellar cells cap the micropylar end of the embryo sac, and are not encroached upon and disintegrated by the growth and expansion of the embryo and endosperm, as is the remainder of the nucellar tissue. A longitudinal section of an ovule containing an immature embryo shows the exact position of these cells, which lie above the embryo and fit closely into the micropyle (25, fig. 63). A similar section of a mature seed (fig. 7) shows these cells surrounding the embryo to the tip of the cotyledons, where they seem to connect with the endosperm. Although the nucellar cells and endosperm appear to merge into a single structure, they differ in that the former does not contain starch grains whereas the latter does, and in that they arise independently. Figs. 10 and 11, longitudinal and transverse sections through the narrow end of a germinated seed, show the large-celled nucellar tissue surrounding the two closely appressed cotyledons to the place where their tip ends are in contact with the endosperm.

The situation in *Dionaea* admits comparison with that of *Peperomia hispidula*, described by JOHNSON (13). In *Dionaea* the food is stored in the endosperm, whereas in *Peperomia* it is stored in the perisperm; in *Dionaea* the embryo is surrounded, with the exception of the tips of the cotyledons, by the persistent nucellar tissue, while in *Peperomia* it is completely invested by the endosperm. JOHNSON suggests that the endosperm of *Peperomia* serves as a medium of transfer of food between the perisperm and embryo, and that it serves as a stopper protecting the germinating seedling from loss of dissolved food, from desiccation, and from the entrance of fungi. It does not seem probable that the persistent nucellar cells in *Dionaea* function as mediums of transfer, since they do not surround the tip ends of the cotyledons. They appear, however, to form an adequate seal against the escape of dissolved food from the endosperm, and most likely prevent the entrance of fungi, as does the endosperm in *Peperomia*.

Seed germination

The first sign of germination of the seed visible from the exterior is the pushing off of the lid by the hypocotyl, at the lower end of which the primary root is developing. This lid, derived solely from



FIGS. 7-14.—Sections of seed and stages in its germination: fig. 7, longitudinal section of mature, latent seed; fig. 8, detail of single endosperm cell containing starch grains; fig. 9, longitudinal section of entire seed and seedling in early stage of germination; fig. 10, detail from fig. 9 showing end of cotyledon and tissues surrounding it; fig. 11, cross-section of seed and seedling at level indicated by dotted line in fig. 9; fig. 12, longitudinal section of seed and seedling at approximately stage shown in fig. 2; fig. 13, cross-section of cotyledon; fig. 14, cross-section of primary root (*c*, cotyledon; *e*, endosperm; *i*, inner seed coat; *l*, seed lid; *mx*, metaxylem; *n*, nucellar tissue; *o*, outer seed coat; *p*, phloem; *px*, protoxylem; *v*, cavity of vascular bundle; *z*, papillate epidermal cell).

the inner integument, often remains attached along one side of the seed (figs. 2, 4, 9). The short hypocotyl and the primary root grow directly downward, and the latter becomes attached to the soil by numerous dark brown root hairs (fig. 1). A longitudinal section of the seed made at this time shows that, in making their exit, the hypocotyl and primary root not only push off the seed lid, but rupture the persistent nucellar layer (fig. 9). The tips of the cotyledons possess slightly elongated, papillate epidermal cells which serve as haustoria, transporting food from the endosperm, with which they are in contact, to the median vascular bundle of their narrow, elongated, basal portion (figs. 9-11). Before the cotyledons emerge, the initial cells of the stellate hairs appear on them, and at approximately the same time they appear on the first secondary leaf developing at the stem growing point (fig. 9).

As the seedling continues its development, the basal ends of the cotyledons, as a result of intercalary growth, elongate and emerge from the seed (fig. 2), become green, and straighten up (fig. 3). The spatulate tips, which originally composed the greater part of the cotyledons, do not increase in size; they remain inclosed and continue to absorb food. A longitudinal section of the seed and seedling (fig. 12) shows the endosperm in direct contact with the tips of the cotyledons, the elongated basal portions of which are studded here and there with stellate hairs, the embryonic leaves arising at the stem growing point, the arched hypocotyl, and finally the primary root protected by the root cap.

One of the cotyledons extricates itself completely from the seed, and the two then diverge to an angle of about 90° , young leaves becoming visible between them (fig. 4). The seed remains attached to one cotyledon even after several secondary leaves have formed (fig. 5); that is, until food absorption is completed. When the seed finally drops off, the spatulate tips of both cotyledons have shriveled and turned brown. By this time the basal part of each cotyledon has reached its full size, varying from 4 to 6 mm. in length, and from 0.1 to 1.2 mm. in width. Stellate hairs and stomata appear on both their upper and lower surfaces, and a transverse section (fig. 13) shows that the epidermis is covered with a thin layer of cutin, and that

each cotyledon contains one principal vein and two smaller veins on each side, surrounded by chlorophyll-bearing parenchyma cells. The arrangement of the vascular tissues of the veins is similar to that ordinarily found in the vein of a secondary leaf of this species.

If the vascular bundles which supply the cotyledons are followed downward, it is found that as they leave the hypocotyl they are inverted, there being no transition region in the hypocotyl. Fig. 9 indicates the position, and figs. 11 and 13 show the endarch collateral arrangement of the vascular elements of the cotyledons. There is no transition region in the hypocotyl, since throughout its entire length, and that of the primary root, the vascular bundles do not alter their course, and orientation of the tissues of the bundles is similar. Since the only notable difference between the hypocotyl and the primary root is the addition of a few xylem and phloem parenchyma cells in the stele of the hypocotyl, a description of the tissues contained in one of these structures will suffice. In a transverse section of the primary root (fig. 14) the following parts are to be distinguished: the epidermis, composed of one layer of cells from which root hairs may arise; the cortex, consisting of three or more layers of parenchyma cells; the endodermis; the pericycle; and the diarch xylem rays alternating with the phloem. No secondary or branch roots are formed. The growing end of the primary root is protected by a root cap, which arises from a common initial zone of the root apex, and is similar to that of the adventive root shown in fig. 33.

The greatest number of root hairs develop on the primary root slightly below the soil line, and are remarkably straight and long (figs. 1-5). They range from 0.4 to 1.9 mm. in length, and are able to resist rough handling; for when soil particles are removed from around them, even with the aid of a camel's hair brush, they escape uninjured. Inasmuch as the chemical composition of their walls seems to be identical with that of the root hairs of the mature plant, the composition of these will be discussed together later.

As the seedling continues to develop leaves, the stem apex moves from between the cotyledons to a position on a level with and external to the proximal end of the cotyledons, and by continued elongation in the same direction, a horizontal rhizome, the apex of which is protected by young leaves, is gradually formed (fig. 6). Adventitious

roots originating from the lower surface of the rhizome, soon begin to appear. Usually six to eight leaves and two or three adventive roots are formed when the seedling, consisting of cotyledons, hypo-



FIGS. 15-28.—Fig. 15, entire seedling, showing, between dotted lines, region from which sections for figs. 16-28 were made; figs. 16-28, series of selected horizontal sections of rhizome of seedling shown, in outline, with vascular content shaded; starting with section shown in fig. 16, sections from which the 12 succeeding figures were drawn are 190, 280, 360, 460, 600, 690, 880, 1080, 1120, 1150, and 1220 μ respectively from it; leaves numbered 1 to 18 and roots lettered A to C in order of appearance.

cotyl, and primary root, begins to shrivel, turn brown, die, and is sloughed off at the proximal end of the rhizome of the now independent plant.

Mature plant

HOLM (11) has called attention to the fact that the first leaves formed, although greatly reduced in size, are identical in structure with the mature leaf, which for decades has held the interest of scientists. Since the anatomy of the blade of the leaf has been investigated and described by OUDEMANS (18), DARWIN (2), KURTZ (15), DE CANDOLLE (1), FRAUSTADT (5), GOEBEL (6), HABERLANDT (9), GUTTENBERG (8), and others, there is no necessity to discuss it here. The basal part of the leaves, rhizome, and roots will however be described. To study the relationship of these parts, 10 μ serial longitudinal sections were cut horizontally (parallel to the soil surface) through a 9-months old plant, beginning at the bases of the leaves just above the rhizome. The space between the horizontal lines in fig. 15 indicates the region of the plant from which the sections were made, and figs. 16-28 show in outline the contents of certain selected sections.

The rhizome usually grows in a directly horizontal plane, but at times the apical end is buried more deeply in the ground than the proximal end. This is particularly true of young plants. The leaves arise in close spiral succession from the apex of the rhizome (figs. 16-28). As they mature they extend first laterally and then upward, the blade and expanded part of the petiole of each unfolding in a circinate manner above ground, leaving only the base of the petiole underground. The petioles of the older leaves, whose bases overlap, inclose and protect the tender embryonic leaves. It is this close set, spiral arrangement which gives the mature plant its characteristic rosette-like appearance. Fig. 29 shows that the base, as has previously been pointed out by various investigators, also serves as a storage organ and contains an abundant supply of starch. The starch grains (fig. 30) are somewhat larger than those found in the endosperm, they are ovoid in outline, and vary from 5 to 15 μ in length. Each petiole may contain one vascular bundle, or in older plants one principal bundle and two smaller, lateral ones on each side. The endarch arrangement of the elements of the bundle (fig. 29) is that typical of the petiole of a leaf. The bundle is completely surrounded and even penetrated by parenchyma cells, which appear to contain a pectic substance.

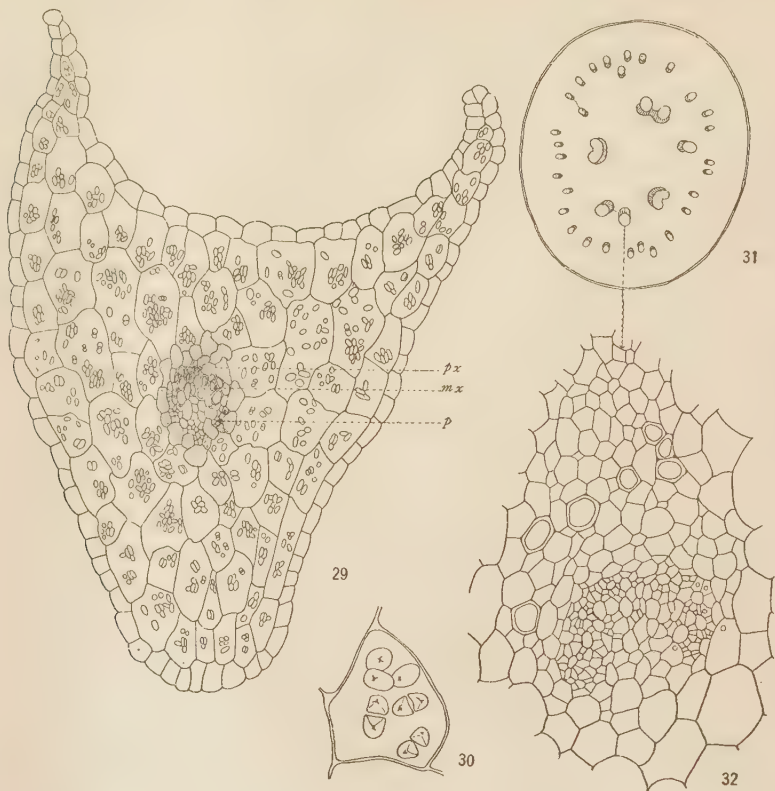
Following the vascular bundle of any leaf to its source (figs. 16-28), it may be observed that it originates from the upper surface of the centrally located vascular tissue of the rhizome. The bases of the petioles of two adjacent leaves not only overlap but are attached, forming a storage and protective covering around the vascular tissue, which is inclosed by a layer of cells, apparently containing a pectic material, similar to that found in the leaf. The rhizome appears to consist of a composite of leaf bases with several vascular bundles coursing through them.

The flower stalk contains a dissected ectophloic siphonostele (figs. 31, 32). This indicates that a similar arrangement of the vascular tissue is entirely possible and even expected in the rhizome.

The roots originate in an almost median line from the ventral side of the vascular tissue, near the apical end of the rhizome. As each develops, it makes its way either through the region where two adjoining leaf bases overlap and are attached to each other, or, less frequently, through the enlarged middle portion of a single leaf base, carrying along a shield-shaped piece of the leaf base (fig. 34), which may be seen surrounding the proximal end of the mature root. Like the rest of the leaf base, this shield-shaped piece has stellate hairs scattered over its surface. Usually three to six functional roots, varying 2-8 cm. in length and 0.5-0.9 mm. in diameter, project downward from the rhizome.

The stele of the root of the young seedling may be diarch, as is the stele of the primary root, or tetrarch (fig. 35), whereas that of the roots of the older plants is most often octarch (fig. 36). This increase in the number of strands is possibly due, as fig. 34 seems to show, to a division of the two primary strands. A root possessing octarch bundles was described and figured by FRAUSTADT (5). Figs. 34-36 show that the roots of *Dionaea* contain a normal series of tissues: epidermis, cortex, endodermis, and stele which consists of pericycle and xylem and phloem strands. The tracheids in each vascular strand, contrary to FRAUSTADT's description, are few in number and irregularly distributed, being separated from those of the adjacent strand by xylem parenchyma. A dark staining material, similar to that in the cells surrounding the vascular tissue of the rhizome and leaf, is found in some of the cells of the cortex, endodermis, and

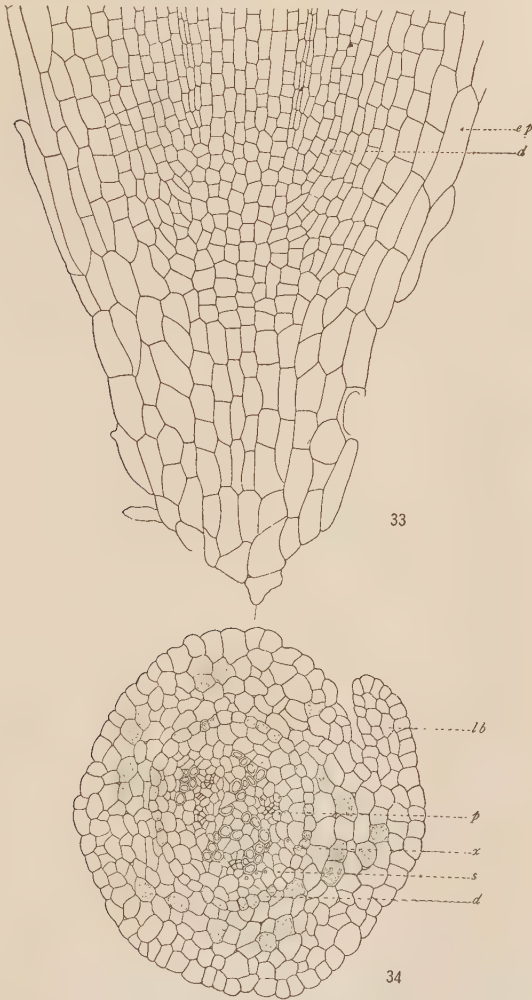
pericycle, and frequently in some of those investing the phloem. In older roots the epidermis and a part of the cortex may be sloughed off, and, when this happens, this dark-staining material appears to collect in the cells of the pericycle on the side where the cortex is



FIGS. 29-32.—Fig. 29, detail of leaf petiole no. 12 in fig. 16; fig. 30, detail from fig. 29 of single starch-containing parenchyma cell; fig. 31, cross-section of flower scape showing arrangement of vascular bundles; fig. 32, detail of single bundle from flower scape (*mx*, metaxylem; *p*, phloem; *px*, protoxylem).

sloughed off (fig. 36). The growing end of the root is protected by a root cap (fig. 33), which originates like the root cap of the primary root from a common initial zone of the promeristem. A few millimeters behind the growing point, root hairs begin to form which, like those of the primary root already described, soon become thick-

walled and turn brown. They may persist throughout the life of the root, and may even be found on the old roots which have ceased to function and are being sloughed off the proximal end of the rhizome.



FIGS. 33, 34.—Fig. 33, longitudinal section of root tip showing root cap arising from common initial zone; fig. 34, detail of root *A* in fig. 21, showing 4 groups of tracheids separated by xylem parenchyma, two distinct phloem strands, and third phloem strand in process of separation (*d*, endodermis; *ep*, epidermis; *lb*, portion of leaf base; *p*, phloem; *s*, pericycle; *x*, xylem).

In an effort to ascertain their composition, the cell walls of the root hairs were tested microchemically as follows: for cellulose, with



FIGS. 35, 36.—Fig. 35, cross-section of root slightly older than one in preceding figure, showing fewer tracheids, more parenchyma, and 4 separate phloem strands; fig. 36, cross-section of octarch root from old plant, showing epidermis and part of cortex sloughed off.

concentrated sulphuric acid, fresh cuprammonia, iodine and sulphuric acid, and with chloriodide of zinc both before and after treatment

with nitric acid and potassium chlorate; for lignin, with phloroglucin and hydrochloric acid, and with aniline sulphate and sulphuric acid both before and after bleaching with sodium hypochlorite; for callose, with resorcin blue; for pectose, with ruthenium red, hydrochloric acid, and potassium hydroxide; for calcium pectate, with ammonium oxalate; for suberin and cutin, with alkanin, chlorophyll, cyanin, and Sudan III, before and after treatment with both potassium hypochlorite and potassium hydroxide. Although the root hairs of *Dionaea* responded to none of these tests, which include those normally used for determining the composition of the cell walls of root hairs, they were finally dissolved after 2 hours' gentle boiling in either a 50 per cent solution of chromic acid or in Schulze's maceration fluid, or after remaining in potassium hypochlorite for 3 full days. Since chromic acid is a recognized test for cutin, and since the root hairs of *Dionaea* responded to this test, they probably contain this substance, although the other tests failed to reveal its presence. The root hairs of *Dionaea*, therefore, appear to be vestigial structures which have ceased to function.

Systematic position of *Dionaea muscipula*

There is some diversity of opinion among recent taxonomists as to the position of the Droseraceae. ENGLER and GILG (4) and RENDLE (21) include the three families Sarraceniaceae, Nepenthaceae, and Droseraceae in the order Sarraceniales. HUTCHINSON (12) includes the Sarraceniaceae and Droseraceae in the Sarraceniales, but places the Nepenthaceae, because of their woody structure, in the order Aristolochiales. DIELS (3), monographer of the Droseraceae for *Das Pflanzenreich*, in discussing the relationship of this family, attaches particular importance to the hypogynous insertion of the parts of the flower, and the truly parietal placentation of the ovules in *Drosera*, and therefore places the Droseraceae under the order Parietales, nearest akin to the Violaceae.² The same scheme is followed by WETTSTEIN (26), who, however, places the Sarraceniaceae and Nepenthaceae in a separate order, the Polycarpicae. While these taxonomists agree in regarding the four genera, *Drosophyllum*, *Dio-*

² DIELS gives an account of the different positions in which the Droseraceae had been placed by taxonomists up to 1906.

naea, *Aldrovanda*, and *Drosera*, as composing the family Droseraceae, SMALL (24) places *Dionaea* in a separate family, the Dionaeaceae. It is of interest to see what light the features of the development of *Dionaea muscipula* recorded in the present paper, as well as in the earlier paper (25), throw on its position in the plant kingdom.

In *Dionaea*, as in *Drosophyllum*, 10-20 (most often 15) stamens are formed, whereas in both *Drosera* and *Aldrovanda* only five are developed. The nuclear phenomena of the microsporocytes of *Dionaea* are essentially like those of *Drosera rotundifolia* and *D. longifolia* described by ROSENBERG (22). Furthermore, judging from ROSENBERG'S figures, the chromosomes of *Drosera* appear to be similar in shape and form to those of *Dionaea*. He gives 10 and 20 as the haploid number of chromosomes respectively in *D. rotundifolia* and *D. longifolia*, whereas 15 is the haploid number in *Dionaea*. The pollen grains of *Dionaea* hang together in tetrads, a characteristic of the entire family. In structure they appear to be similar to the pollen grains of *Drosera squamosa* as described by DIELS (3).

One of the most distinctive parts of the flower of the Droseraceae is the pistil. In *Dionaea* and *Drosophyllum* it is composed of 5 carpels, and contains numerous seeds on a basal placenta. Whether the ovary of *Drosophyllum* is "paracarpous," and bears its ovules without the aid of the vegetative apex of the flower, as described by GOEBEL (7) for *Dionaea*, or whether the vegetative apex shares in the formation of the ovary, has not been reported, nor has the writer had an opportunity to investigate this situation. Judging from DIELS' figures, however, one would be inclined to conclude that they develop as in *Dionaea*. In *Aldrovanda* and in *Drosera*, the ovary is syncarpous, in the former consisting of 5 carpels, in the latter 2-5 (most often 3). In both genera the ovules develop on marginal parietal placentas.

While all four genera have anatropous ovules, there are striking similarities as well as differences in the development of the ovules of *Dionaea* and of *Drosera*. In *Dionaea* the hypodermal archesporium divides to form two or sometimes three layers of parietal cells above the embryo sac, whereas in *Drosera* (PACE 19) parietal cells are commonly not formed, although sometimes a single layer develops between the epidermis and the mother cell. Furthermore, the enlargement of the outer layer of nucellar cells of *Dionaea* resembles that

of *Drosera rotundifolia* described by Miss PACE, but the fate of the cells in *Dionaea* (25) is different from that suggested by her for *Drosera*. Moreover, a comparison of the mature embryo sac of *Dionaea* (25) with that of *Drosera* (19) shows the two to be similar. *Dionaea* develops a seed lid not markedly different from that in *D. rotundifolia* described by NETOLITZKY (17).

Dionaea is the only one of the Droseraceae in which the persistent nucellar tissue has been observed and described. The slides of *Drosera rotundifolia* made by PETERS (25), when compared with slides of *Dionaea*, show that the endosperm of the two passes through practically the same stages of karyokinetic differentiation and development. The embryo of *Dionaea*, as is true of that of the other members of the family, is small, and lies at the base of the seed in direct contact with the copious endosperm.

A comparative study of germination of the seeds of the four genera of the Droseraceae shows the following gradation in the development of the primary root and cotyledons. (1) Neither *Aldrovanda*, as described by KORZCHINSKY (14), nor *Drosera*, as described by HEINRICHER (10) and later by DIELS (3), develops a vigorous primary root; instead, each forms a rudimentary root which functions for a brief time only. (2) *Dionaea*, according to HOLM (11), develops a primary root, which, as the present investigation shows, ceases to function and is sloughed off with the cotyledons after leaves and adventitious roots have formed and the plant has become independent. (3) *Drosophyllum*, according to PENZIG (20), develops a primary root which persists. On the other hand, the four genera vary with respect to the function and development of the cotyledons: in *Aldrovanda*, according to KORZCHINSKY (14), and in *Drosophyllum*, according to PENZIG (20), the cotyledons remain within the seed and absorb food from the endosperm; whereas in *Drosera*, according to HEINRICHER (10) and DIELS (3), and in *Dionaea*, only the tips of the cotyledons do this. The remaining and greater part of the cotyledons emerge and carry on the process of photosynthesis. Germination of the seed of *Dionaea* closely resembles that of *Sarracenia* and *Darlingtonia* described by MACFARLANE (16).

Since there are numerous characters upon which the four genera agree exactly, since there is a smaller number upon which at least two genera agree, and since there are only a few upon which all the

genera differ, it seems logical to concur with those who place *Dionaea* among the Droseraceae, and divide the family into the four genera *Drosophyllum*, *Aldrovanda*, *Dionaea*, and *Drosera*. Furthermore, a comparative study of the morphology of the flowers of the Droseraceae and the Sarraceniaceae and Nepenthaceae, although showing that these differ as to number of stamens, number of carpels, and placentation of ovules, definitely indicates their affinity. Among the Sarraceniaceae the stamens vary from 10 to ∞ ; in *Sarracenia* there are 70–80, which, according to SHREVE (23), originate as ten groups of primordia; in *Darlingtonia*, according to MACFARLANE (16), 15 is the typical number formed. Among the Droseraceae, on the other hand, the stamens range from 5 to 20; in *Dionaea* and in *Drosophyllum* there are 10–20 (most often 15), which, in *Dionaea* and probably in *Drosophyllum*, originate as in *Sarracenia* as ten groups of primordia; in *Drosera* and in *Aldrovanda* 5 are regularly produced. The pistil shows the following variations: in *Aldrovanda* it consists of 5 and in *Drosera* 2–5 (most often 3) united carpels, which bear their ovules on marginal, parietal placentas; in *Drosophyllum* and in *Dionaea* it is made up of 5 carpels, which develop ovules on their united upraised bases; in *Sarracenia* and *Darlingtonia* it has 5, and in *Heliamphora* 3 united carpels, which grow inward and develop their ovules on axillary placentas. Apparently, therefore, the three families should be placed in the order Sarraceniales.

Summary

1. Germination of the seed and development of the seedling of *Dionaea* proceed as follows: the hypocotyl and the primary root elongate, rupture the nucellar cap, and push aside the seed lid; the cotyledons partially emerge, turn green, and straighten up, carrying the seed with them; one cotyledon releases itself completely and the other remains attached by its tip end, the two then diverging and young leaves appearing between them. The stem apex, which gives rise to leaves in spiral succession, gradually moves horizontally from between the cotyledons, forming a subterranean rhizome from the lower surface of which adventive roots arise; the cotyledons, hypocotyl, and primary root finally cease to function and are sloughed off the basal end of the rhizome of the now independent plant.

2. The main aspects of the anatomy of the seedling are as follows: the hypocotyl and the primary root are similar in structure, both having epidermis, cortex, endodermis, pericycle, and a diarch stele; there is no transition region in the hypocotyl, the vascular bundles being inverted where they enter the cotyledons; the cotyledons, with stomata and stellate hairs present on both upper and lower surfaces, have a median collateral endarch vascular bundle from which two or more lateral branches extend.

3. The rhizome appears to consist of an agglomeration of overlapping undiverged leaf bases with several vascular bundles coursing through them.

4. The stele of the root of a young plant is usually tetrarch, whereas the stele of the root of a mature plant is most often octarch.

5. The root hairs, which begin to form a few millimeters behind the growing point, soon turn brown and become thick-walled, often persisting throughout the life of the root. Of the microchemical tests used to determine the composition of their cell walls, the chromic acid test for cutin alone gave positive results. They appear, therefore, to be vestigial structures.

6. The evidence gained from a comparative study of the development of *Dionaea* and the plants closely related to it indicates that *Dionaea* should be placed in the family Droseraceae and in the order Sarraceniales.

For suggesting the subject of this paper and for helpful criticism, the writer makes grateful acknowledgment to Professor DUNCAN S. JOHNSON.

BAYLOR UNIVERSITY
WACO, TEXAS

[Accepted for publication August 29, 1930]

LITERATURE CITED

1. DE CANDOLLE, C., Sur la structure et les mouvements des feuilles du *Dionaea muscipula*. Arch. Sci. Phys. Nat. 55:400-431. 1876.
2. DARWIN, C., Insectivorous plants. London. (pp. 286-320). 1875.
3. DIELS, L., Droseraceae. ENGLER, A., Das Pflanzenreich IV. 112:1-136. 1906.
4. ENGLER, A., and GILG, E., Syllabus der Pflanzenfamilien. Berlin. 1924.

5. FRAUSTADT, A., Anatomie der vegetativen Organe von *Dionaea muscipula* Ellis. Cohn Beiträge Biol. Pflanzen 2:27-64. 1877.
6. GOEBEL, K., Pflanzenbiologische Schilderungen. Marburg. (pp. 57-72). 1893.
7. ———, Organographie der Pflanzen. Jena. (pp. 741-742). 1898-1901.
8. VON GUTTENBERG, HERMANN, Die Bewegungsmechanik des Laubblattes von *Dionaea muscipula* Ell. Flora (Neue Folge) 18-19:165-183. 1925.
9. HABERLANDT, G., Sinnesorgane im Pflanzenreich. Leipzig. (pp. 108-117). 1901.
10. HEINRICHER, E., Zur Kenntnis von *Drosera*. Ferdinandeum Zeitschr. Innsbruck 46:1-25. 1902; 47:300-307. 1903.
11. HOLM, THEO., Contributions to the knowledge of the germination of some North American plants. Mem. Torr. Bot. Club 2:57-108. 1891.
12. HUTCHINSON, J., The families of flowering plants. I. Dicotyledons. New York. 1926.
13. JOHNSON, D. S., Studies on the development of the Piperaceae. Amer. Jour. Bot. 1:357-397. 1914.
14. KORZCHINSKY, S., Über die Samen der *Aldrovanda vesiculosa* L. Botan. Centralbl. (N. S.) 27-28:334-335. 1886.
15. KURTZ, F., Zur Anatomie des Blattes der *Dionaea muscipula*. Archiv. Anat., Physiol. Wiss. Med. Reichert Du Bois-Reymond. (pp. 1-29). 1876.
16. MACFARLANE, J. M., Sarraceniaceae. ENGLER, A., Das Pflanzenreich IV. 110:1-38. 1908.
17. NETOLITZKY, F., Anatomie der Angiospermen-Samen. LINSBAUER, K., Handbuch Pflanzenanatomie 10:146-149. 1926.
18. OUDEMANS, C. A. J. A., Over de Prikkelbaarheid der Bladen von *Dionaea muscipula*. Verslagen. Medeldeel. K. Akad. Wetensch. 9:320-436. 1859.
19. PACE, LULA, *Parnassia* and some allied genera. BOT. GAZ. 54:306-329. 1912.
20. PENZIG, O., Untersuchungen über *Drosophyllum lusitanicum* Link. Breslau. 1877.
21. RENDLE, A. B., The classification of flowering plants. II. Dicotyledons. Cambridge Univ. Press. (pp. 193-199). 1925.
22. ROSENBERG, O., Cytologische und Morphologische Studien an *Drosera longifolia* × *rotundifolia*. Kungl. Svenska Vet. Handlingar 43:4-64. 1908.
23. SHREVE, F., The development and anatomy of *Sarracenia purpurea*. BOT. GAZ. 42:107-126. 1906.
24. SMALL, J. K., Flora of the southeastern United States. New York. (pp. 492-493). 1903.
25. SMITH, CORNELIA MARSCHALL, Development of *Dionaea muscipula*. BOT. GAZ. 87:507-530. 1929.
26. VON WETTSTEIN, R., Handbuch der Systematischen Botanik. II. Leipzig. 1924.

VITA

Cornelia Marschall Smith was born October 15, 1895, in Llano, Texas, where she received her elementary and high school education. In 1918 she was granted her B.A. degree from Baylor University, having majored in botany under Professor Lula Pace. Later she continued the study of plants with Professors Charles J. Chamberlain and W. J. G. Land at the University of Chicago, receiving her Master's degree from that institution in 1923. She was married to Charles G. Smith on September 9, 1926. The following two years were spent in Johns Hopkins University, where she studied with Professors Duncan S. Johnson and Burton E. Livingston. In June, 1928, she was granted the Ph.D. degree from that institution.

